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THE QUARTERLY REVIEW OF BIOLOGY

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THE QUARTERLY REVIEW *of* BIOLOGY



THE "CONCEPT OF ORGANISM" AND THE RELATION BETWEEN EMBRYOLOGY AND GENETICS

PART I

By J. H. WOODGER

University of London

IT HAS become almost a commonplace of the times in which we live to demand that knowledge—scientifically garnered and sifted—should be applied in all human undertakings. It is no longer considered sufficient, as it was in former times, to be guided by "intuition" or rule of thumb tradition, however successful this may be. No. Nowadays it is held that the process in question, whatever it is, must first be subjected to scientific analysis, and the work carried out in the light of the knowledge thus obtained. Now it seems at first sight a curious fact that the very people who are responsible for this change, or at least for providing the knowledge upon which it is based, do not apply the principle to their own activities. That is to say, the people who pursue natural scientific knowledge may be said, as a rule, and from one point of view at least, not to know what they are doing in somewhat the same sense in which a cook may be said not to know what she is

doing when she uses baking powder. She knows that with this ingredient the buns will "rise," and so long as this is the case why need she concern herself with the properties of CO_2 or the laws of gases? In the same way, so long as the investigator of nature continues to make discoveries (and the volume of papers issued in the quarterly journals shows no sign of decline) there would seem to be no occasion to deflect attention from the business of investigating nature to matters relating to the process of investigation itself.

But the situation is complicated in various ways which require disentangling. In the first place the biological student does in fact receive instruction in the use of instruments, dyes, etc., based upon knowledge obtained by a scientific study of such things, and he is also required to know a great deal about other branches of natural science which will be involved in his biological investigations. But there are other important points which are

liable to be overlooked. It is generally believed that the business of the biologist is not exhausted when he has made his observations and recorded them in the quarterly journals. Those journals are so many store-houses of data in a raw state and, in a sense, in an "unavailable" form,—in a form, that is to say, in which they are of little interest or value to anyone but the small group of specialists in the particular branch of biology concerned. Before such knowledge can become of wider availability it must be subjected to a *further* process through which it becomes articulated into a wider body of knowledge and brought into relation with other branches of the subject. Thus there appear to be two different but related processes: investigation and interpretation, and these two processes appear to be different in their nature, their outcome, and in the "canons" which regulate them. The investigatory process reduces at bottom either to observing organisms or parts of organisms in their natural relations, or to altering their natural relations in a systematic way, and recording the results. And, since the primary aim of investigation is discovery, whatever procedure leads to discovery will be accounted *good*, and whatever methods fail to achieve this end will be rejected. Thus, as far as methods of investigation are concerned (whether this refers to technical processes or to intellectual tools, i.e., "working hypotheses") heuristic success will be the touchstone by which the investigator will measure all things.

So much, then, for the criteria by which we judge the value of a method of investigation. But how do we judge whether the *outcome* of such methods is "good"? The outcome of an investigation is a series of propositions which are conveyed to the world at large by means of printed sen-

tences in the quarterly journals, and the primary requisite of such propositions is that they should be *true*. The majority of such propositions simply state what did in fact happen in a certain laboratory on a certain date under more or less definitely known conditions. We all know what is meant by saying that such records are true, and no honest man would include false propositions in his report if he knows they are false. But when we consider the process of interpretation and its outcome the situation is different. Here it is a question of intellectually mastering the data furnished by the former process—of systematizing the propositions already obtained in the form of general propositions which are hypothetical in the sense that we do not *know* that they are true, although we know that they are either true or false. And we are usually in the position that it may be possible to discover whether they are false, but it will never be possible to *know* that they are true. And by knowing I *mean* knowing, *sensu stricto*, as contrasted with supposing or believing.

Now it is clear that the sort of systematized knowledge about instruments and dyes, etc., which the investigator uses to guide him in his pursuits, is natural scientific knowledge. It is applied physics and chemistry. But the sort of knowledge required for the guidance of the process of interpretation will be knowledge about the properties of *knowledge itself*, and will not be natural scientific knowledge. It seems to be the case as a general rule that the people who pursue natural scientific knowledge never pay much attention to knowledge about knowledge itself, and the people who make knowledge itself an object of scientific investigation do not always know much about the subject matter of natural scientific knowledge. It is this state of affairs which is

responsible for a situation comparable to that of the cook and the baking powder. Everyone recognizes the desirability of knowing something about the physical instruments used in scientific investigation, but the importance of understanding the properties of the intellectual tools involved—concepts, propositions, principles of inference, "working hypotheses," postulates, etc.—is much less clearly appreciated. And from the standpoint of the process of *interpretation* this *may* be a misfortune.

An excellent illustration of the desirability of devoting some attention to these matters is furnished by the history of comparative psychology as related in a recent article in this REVIEW by C. J. Warden (11). The point of special interest in this example is that the position reached at the end of the story could have been grasped perfectly well at the beginning if more attention had been paid to an understanding of knowledge itself, and if certain speculative assumptions had not been permitted to influence empirical investigation. Such assumptions always have their "good" and "bad" sides. On the one hand they often lead people to make certain investigations which they would not otherwise have done, and hence lead to discoveries, and they are therefore important heuristically. But they are bad if they are allowed to influence the outcome of an investigation, if they lead to too great a restriction of the field of interest, and to a one-sided selection of evidence. All these points are illustrated in the paper referred to.

It is important to distinguish three kinds of assumptions. First, there are those commonly called "working hypotheses," and obviously the first requisite of such an assumption is that it *will* work, i.e. is such that it can be put to an empirical test which will definitely *disprove* it if it is

false. We cannot put it more positively than that because, if the test does *not* disprove it, it does not follow that it is true. This happens, for example, in the case of hypotheses which assert the existence of entities which can never be observed. A good example of such a hypothesis which *could* be disproved is furnished by Weismann's hypothesis of development. But there are also hypotheses of a totally different character which are such that no experimental test can *possibly* be devised which would decisively disprove them if they were false. Of these there are two distinct kinds. First, there are those assumptions which, if false, would render nugatory all intellectual activity. In regard to these, although we have no *reason* for believing them to be true, we yet have a very strong *motive* for believing them to be so. In natural science we adopt certain assumptions of this kind: they are *postulates* necessary for the possibility of knowledge. The second type of untestable assumptions embraces those which are not necessary for the possibility of knowledge. These might be distinguished as *metaphysical* assumptions, and it is clear that if they are admitted into science their proper character should not be forgotten, especially if they are taken over uncritically from common-sense beliefs. Also regarding assumptions in general, it is evident that if you *assume* a certain proposition *p*, then any proposition which depends for its truth upon the truth of *p* must itself be hypothetical and cannot be regarded as one of the facts which are the outcome of your investigation. And if it is considered necessary to assume that *p* is true, if even the possibility of its falsehood cannot be entertained, then clearly the aim and outcome of your investigation cannot be to support or to deny *p*, but must be confined to propositions which

will be true only *if* p is true. It is necessary to draw attention to these points because they are involved in what follows and have often been neglected.

There is another feature of natural science in regard to which "knowledge about knowledge itself" is important. We distinguish between experimental and theoretical physics but we make no such distinction in biology. There are biological theories in abundance but no theoretical biology. There are books in plenty on experimental embryology but none on theoretical embryology. Why is this? One reason seems to be that biological knowledge is believed to progress by "observation and experiment." It is commonly taught in popular books on the history of natural science that at the Renaissance someone discovered that observation and experiment were essential to the attainment of natural knowledge, and that it was this which distinguished the later centuries from the Middle Ages. This is perfectly true, but it is a half-truth, and half-truths are usually dangerous. What is here omitted is every bit as important and essential to scientific progress as what is asserted. If physics had proceeded on these lines there would never have been any theoretical physics, and if biology does not pay attention to what is here omitted it is doubtful whether there will ever be any theoretical biology. We therefore require to discover what this other ingredient may be. Theoretical physics is sometimes called *mathematical* physics, and this seems to have led some biologists to suppose that all we have to do is to "apply" mathematics to biological data and theoretical biology will automatically emerge. This is, I think, a mistake founded upon a too simple and too superficial view of the situation. It is not so much the mathematical laws of physics as such that we require, but the

mathematical *method* in the broadest sense, and this is quite a different thing. Natural scientific knowledge springs from a fertilizing union of two "realms": the realm of sense-experience or perception, on the one hand, and the "logical realm" or the realm of abstract logical entities and relations, on the other. The mistake of the Middle Ages was to neglect the former and to attend to only a very restricted aspect of the latter; the mistake of biology has been to concentrate entirely on the former and to use the latter only unconsciously or "intuitively." The success of theoretical physics has depended on the fact that, aided by pure mathematics, it has been able to explore and combine both. But it is a great mistake to suppose that mathematics as ordinarily understood exhausts the logical realm. It is now recognized that it represents only certain aspects of it, and this fact has come to light in comparatively recent years as a result of investigations into the nature of pure mathematics itself. Knowledge about knowledge itself is very important for understanding the logical realm.

II

Biology at the present day seems to be passing through a critical period in which new ideas are clamoring for attention, whilst their recognition is being retarded by various conservative factors. In various quarters signs are discernible that this is slowly becoming realized. As far as *investigation* is concerned the turn of the tide took place some time ago, when what has been called the "romantic" period came to an end with the tardy recognition that experiment was required for further progress. But accompanying these changes in the standpoint of investigators there has been no fundamental change in biological *interpretation*. It is here that

change is confronted with the most formidable obstacles. It is easy enough to appreciate the need for supplementing observation by experiment, but it is quite another thing to foresee the need for a revision of our ways of thinking, and a very difficult thing indeed to carry out such a revision. These things appear to be better understood in Germany than in the English-speaking countries. In England it is not among men of science that we find most interest taken in the newer biological ideas. But in 1919 J. Schaxel (10) published a book in which he pointed out the exceedingly heterogeneous nature of biological thought, drew attention to its inconsistencies, and urged the need for a critical sifting of its fundamental concepts. The first edition was out of print before the end of the year and a second was issued in 1922. It is difficult to imagine such a book passing through two editions in England. Schaxel's chief aim was to drive home the necessity of understanding that strictness of *thought*, as well as exactness of investigation, is essential if biology is to emerge from the morass into which its "careless *Begriffsrromantik*" (as Schaxel calls it) has brought it. Since the first publication of this book Schaxel has edited a series of *Abhandlungen zur theoretischen Biologie*, to which a number of German thinkers have contributed, and it is among these that the reader may discern the signs of reawakening to which reference has been made. These writers all recognize that a given set of assumptions will commit you to a certain definite set of conclusions. But in biology our fundamental notions are for the most part so vague and lacking in precise definition that it is impossible to work out their logical consequences to any clear cut result, as any one will have realized who has attempted to discover the precise points at issue in the traditional biological

controversies. The German authors make a distinction between "law" (*Gesetz*) and "rule" (*Regel*) which recognizes the distinction between what I have called the logical and empirical realms. By a *law* they mean an *a priori* logical system capable of strict deductive development, although this need not be "mathematical" in the narrow sense, but may be "logistic" in the sense of C. I. Lewis (9). By a *rule* these authors simply mean an empirical inductive generalization. But by no means all German biological writers either make this distinction in the above way or realise its importance. Thus B. Dürken (4) writes:

It must never be forgotten that the task of the exact investigation of nature does not consist in trying to explain nature by deduction from general principles, and so adapting the facts to preconceived opinions; but lies in the attempt to obtain a general view of natural occurrences inductively from the greatest possible number of isolated facts.

Now this is certainly not the way in which physics developed, as illustrated, for example, by the procedure of Galileo and Kepler. It represents only one aspect of the process. Induction is necessary but not sufficient. It will give us biological theories but not theoretical biology. Only if and when a system of logical relations is discovered from which the empirical generalizations can be deductively developed and into which the biological concepts enter as values of the logical variables will anything approaching theoretical biology, which is at all comparable with theoretical physics, be possible.

The authors in Schaxel's *Abhandlungen* deal, for the most part, with the clarification of biological concepts, a most necessary preliminary, and also with the working out of new ones. And if it is possible to pick out one theme which is especially prominent in these discus-

sions it seems to be one which turns on the question whether we are to regard the organism *as* an organism or not, and on the difficulties which present themselves when we answer this question in the affirmative. To an outsider it will seem strange that there should be any such question, but it admits of course of a simple historical explanation. In the past the concept of organism has not been employed by the majority of biologists, but instead, owing to the methodological success of the notions bequeathed to us by René Descartes, organisms have been more commonly regarded as, in some sense, machines, although in what sense has not always been clear. I have attempted to clarify this question elsewhere (17). To discover what the "concept of organism" means at the present day one must consult, not a biologist, but certain types of philosopher, or, curiously enough, certain types of mathematical physicist. In histories of biology in the dim future there will probably be a chapter entitled "The Struggle for Existence of the Concept of Organism in the Early Twentieth Century," which will relate how this concept came to be neglected on account of the influence of Descartes, how the metaphysics of natural science in the Nineteenth Century so completely dazzled biologists that they never dreamed of regarding organisms as being anything but swarms of little invisible hard lumps in motion, and how the first blossoming of the concept of organism towards the end of the century was nipped in the bud by the mismanagement of those who advocated it. The rest of the chapter remains to be written. It is of no use dogmatizing or getting emotional about it.

The story is tolerably simple when it is disengaged from the learned verbiage in which it is apt to be concealed. Descartes,

who invented the machine theory, understood perfectly well that a machine presupposes a mechanic, but where was the mechanic of the living machine? Descartes was a pious man, and was in the habit of appealing to God to get him out of difficulties. It was to God that he appealed to overcome the difficulty of discriminating between dreams and waking experience, and thus to reassure himself of the existence of an external world, after the celebrated method of doubt had been pushed too far. It was to God that Descartes appealed to furnish the missing mechanic for the organic machines. That was in the days when "development" meant "evolutio." Thus Descartes set the fashion of regarding the organism as a machine with a transcendent mechanic or "organizing principle" and this practice has been followed by some biologists ever since. But others—and they form the majority—who had no use for transcendent principles, and who lacked the Cartesian consistency, have contrived to get on with a machine *without* a mechanic, and this, as Euclid says, is absurd. But nevertheless this view *worked*: that was the main thing, although it did not alter the fact that it was absurd. Only a few thoughtful people have seen that it is absurd. To Driesch belongs the credit of seeing this more clearly than anyone else and of keeping people constantly uneasy about it. But instead of throwing over the machine theory he retains it with a transcendent mechanic, although not in the Cartesian manner. This naturally so disgusted the rank and file that they failed to give sufficient attention to Driesch's admirable critical work. Thus the concept of organism failed to receive due attention because Driesch's mechanic was of no help from the scientific standpoint, however successful it may have been from the metaphysi-

cal. But nevertheless some of Driesch's arguments are important and we cannot refute them merely by expressing our dislike of their supposed consequences.

In England the story has taken a different course. Here the shortcomings of the machine theory have been appreciated by a physiologist, J. S. Haldane. He has perceived not only the contradictions of the machine theory but also the difficulties of appealing to a transcendent mechanic. Accordingly he has urged the abandonment of the machine theory and the desirability of treating the organism *as* an organism. Why is it then that he has had just as small a following as Driesch? The chief reason seems to be that J. S. Haldane has been content to use the "concept of organism" intuitively in his own work without attempting to give it an abstract formulation. His critical arguments are not so compelling as those of Driesch for a similar reason, and his assertions regarding what he wishes to put in the place of the machine theory are somewhat vague, and require "sympathetic" interpretation. Both of these eminent writers seem to have shown a deplorable lack of understanding of the psychology of the scientific investigator. Moreover, obstacles have also been created by the horrible ambiguity attaching to the term "mechanistic." Abandoning the machine theory does not necessarily mean abandoning "mechanism" in *all* its various meanings, as J. S. Haldane seems to suppose. Neither is "physical" synonymous with "mechanical." It is important to understand this. But Haldane has had the depth of vision to see that far more than a mere re-shuffling or re-definition of biological concepts is involved in the reform of biological thought. It requires investigations which go below the specifically biological level into problems concerning "knowledge about knowledge

itself," and it is the difficulties attendant upon an intellectual upheaval of this kind which are largely responsible for the backwardness of the revolution in biological thinking. We do not always appreciate the harm done by the camp followers of great men, in whose hands discoveries which were at first fluid and tentative become petrified into dogmas which create obstacles to further progress. In this way the logical dogmas of Aristotle, the psychological dogmas of Locke, the biological dogmas of Darwin, and above all, the physical and metaphysical dogmas of Descartes are all operative to-day even in the biological sciences. Such dogmas may constitute intellectual blind-spots preventing us from realizing to what a great extent we are free to explore new ways of thinking if new empirical data should require them. But as tentative assumptions harden into dogmas which are never examined our thoughts become encrusted with layers of intellectual rubbish which require the labors of an intellectual Hercules for their proper purgation. Among modern writers who have felt the need for such an undertaking few are better equipped than A. N. Whitehead, and the reader who wishes to learn what it involves, and why it is necessary, cannot do better than read the splendid first two chapters of that author's *Concept of Nature* (14). I have discussed some of these problems from the biological standpoint in a recent publication (18).

Perhaps we can apply G. K. Chesterton's remark about Christianity to the "concept of organism": "It has not been tried and found wanting; it has been found difficult and not tried."

III

After these necessary preliminaries I turn now to the chief task of this paper.

I wish first to introduce and define clearly some concepts which appear to be involved in the "concept of organism," to analyse a type of logical order which appears to be exemplified in the organic realm, to examine the use of the causal postulate in biology, and then to apply all this to certain difficulties in embryology and genetics in order to trace them to their sources, and to enable us to think clearly about them. It is hopeless to work in a fog from lack of proper analysis of your thought, and it is equally hopeless to pursue a policy of obscurantism which refuses to allow awkward questions to be raised and openly examined. The situation is complicated and its difficulties are enhanced by the impossibility of saying everything at once. It will be necessary to explain first a number of seemingly disconnected notions and then to try to bring them together at the end.

The concept of organism requires a number of subsidiary notions such as "organic whole," "organic part" and "organic relation." Also an organism exhibits what I shall call "hierarchical order." It is easy enough to see "intuitively" what is meant by these terms; there has been a good deal of vague talk from time to time about "the whole being more than the sum of its parts," etc.; the difficulty is to make these notions precise in order to enable us to see how we can use them for scientific purposes. Intuition is the indispensable cutting edge of intellectual inquiry, but the ground won is not consolidated until it has passed from the stage of intuitive apprehension to that of logical analysis.

I shall first try to state quite abstractly what is intended by "hierarchical order," and by abstractly I mean without reference to any *particular* exemplification. We have to investigate hierarchical order as it is in the "logical realm" in its most

generalized form. Only then can we profitably discuss its empirical exemplifications. Any reader who finds difficulty in following the abstract exposition can easily make for himself a "particular exemplification" by simply drawing a square on a piece of paper, dividing it into four quarter squares, then dividing each of these into four and so on *ad libitum*. But it must be remembered that this is only a particular exemplification, and that hierarchical order has, as such, nothing to do with "space."

The notion of order requires "individuals" or single entities for thought, classes of such, and relations. In hierarchical order we begin with a single individual which will be symbolized by W . This is analysable into individuals called members (m or M) which fall into classes of two kinds called *levels* (L), and *assemblages* (A). There is also a fundamental relation (R_H) in which the members stand to one another, and upon which the whole hierarchical type of order depends. (This will be the relation "being a quarter of" in the case of the square.) We proceed to the following definitions:

Level: A level is a class of members of W which exhaustively divides W and is such that no member of the class stands in the relation R_H to any other member of the class. In any hierarchy there are at least two levels.

Highest level: One level is such that none of its members stand in the relation R_H to any other member, but each stands in the relation R_H to W . This may be called the highest level.

Lowest level: if there is any level which is such that its members are incapable of further analysis this constitutes the lowest level.

Next highest level: if m is any member of a given level L then there is one and only

one level (other than L) containing one and only one member M such that m stands in the relation R_H to M . This is the next highest level above L .

Assemblage: if we take any member M belonging to any level except the lowest it will be analysable into a class of members $m_1, m_2, m_3, \dots m_n$, which is such that it exhausts the member M from which we begin, all its members stand in the relation R_H to M , and none of them stand in the relation R_H to any other member of W . Such a class obtained by analysing any member is called an assemblage.

Thus each member of a given level L is analysable into an assemblage A of members each standing in the relation R_H to A , and since (by definition) none of the members of A stand in the relation R_H to any other member, they constitute, with the members into which the other members of the level L are analysable, a new level, which is the *level next below* L . In this way we can proceed until we reach the lowest level.

It will be found that a given member m cannot be a member of W without standing in the relation R_H to some member M belonging to the level next above its own level unless m belongs to the highest level.

In addition to the generating relation R_H there will also be relations (R_L) between members of a level, and relations (R_A) between members of an assemblage.

It is important to note that a given member can always be regarded from three points of view: (1) from the point of view of its membership of a level, i.e., its R_L relations; (2) from the point of view of its entering, with other members of its level, into the constitution of a member of the next highest level, i.e., its R_H and R_A relations; and (3) from the point of view of its analysis into an assemblage of members of the next lowest level in their R_A relations.

This brief account by no means exhausts the subtleties of hierarchical order but will suffice for present requirements. We can turn now to see how it is exemplified in nature. I follow the view of A. N. Whitehead that nature is primarily analysable into spatio-temporal entities (which he calls "events") which pass, and their characters (his "objects") which endure, i.e., can "be again." If we apply hierarchical order to spatio-temporal entities, then W will be a spatio-temporal *whole*, analysable into members which can properly be called *parts*. Moreover hierarchical order may be generated in nature through a temporal process, and this may happen in two ways. (1) by the coming together into R_H relations of originally separate entities which thus become members of a hierarchy constituting a new whole; or, (2) by the division of an original single whole into parts standing in R_H relations. The first case is exemplified in crystallization, the second in the process of development of a metazoan organism. If by a "cell" you mean a spatio-temporal entity which is such that in visual perception it is characterized by an "object" or "pattern" roughly indicated as analysable into a nucleus and cytoplasm, then it is easy to see that in a metazoan animal the parts recognizable as cells constitute a level which is homogeneous with respect to the type of organization of its members. But there may be, and usually are, parts constituting a higher level, namely parts analysable into cells, and these will be cell-assemblages or *cellular parts*. Also each cell is analysable into an assemblage of *cell-parts*, and these are ultimately analysable into the entities with which chemists deal. In cases where it is important to bear in mind that we are speaking of parts it will be desirable to refer to cells as "non-cellular parts" (following the precedent

of those who speak of protozoa as non-cellular), since the cell-type of organization characterizes wholes (e.g., germ-cells and protozoa) as well as parts, and from the organic standpoint it is important not to confuse parts and wholes since they have very different properties. Thus we have three levels recognizable in perception: (1) that of which the members are cellular parts; (2) that of which the members are non-cellular parts (cells); and (3) that of which the members are cell-parts. Below this there may of course be any number of levels not accessible to perception, and about which we can only assert hypothetical propositions. It is interesting to note that in a metazoan animal there may be spatial parts which lie outside the organic hierarchy, since they do not stand in an R_H relation to other parts, and parts do not stand in such relations to them, for example, the matrix of cartilage, and such parts are always "dead."

So far we have merely noted some obvious points about hierarchical order in the spatial organism. But this is an abstraction resulting from the separation of space from time, and there is no such thing as a living organism in abstraction from time. The living organism is always a four-dimensional entity with temporal as well as spatial extension. The purely spatial three-dimensional organism is the organism considered at a moment, and a moment is an "ideal" to which we approximate by a progressive diminution of the time-dimension in accordance with the method of extensive abstraction, as Whitehead (15) has shown. If now we conceive the organic realm from the four-dimensional standpoint we shall see other ways in which hierarchical order is exemplified. It is generated through the process of reproduction, by which an organic race comes into being. If we

consider this four-dimensionally we see that if we begin with a single organism (or pair of organisms) a hierarchy is generated in which the original starting point constitutes the highest level, the F_1 generation constitutes the next level and so on. The relation R_H is the relation "being an immediate descendent of," and the assemblages in each level except the first two will be "families," i.e., the immediate descendents of a given member (or pair) of the level immediately above the one in question. Such a hierarchy would be a genetic hierarchy.

Cell-division, as already mentioned, also generates a hierarchy. Considering this from the four-dimensional standpoint we see that starting from a single cell we obtain a hierarchy in which the highest level is this starting point, and each assemblage contains only two members (when division is binary). The R_H relation will be "being an immediate cell-descendant of." The second level will contain one member (an assemblage of two cells), the next two, and so on. If the cells always divide simultaneously those belonging to the same level will always lie in the same "moment." Now there are two possibilities: (1) either the members characterized as cells are single individual organisms as in the protozoa, or (2) they remain in a certain relation to one another so as to constitute not wholes but parts of one organic whole; we then have the "spatial" hierarchy generated, as already mentioned, in the process of development in metazoa.

When a natural entity is divided there are always two possibilities: (1) the two parts may be equal in the sense of having precisely the same properties; or (2) they may be unequal and have different properties. If the process of division in the protozoa is equal in the above sense the individuals in any level will differ from

one another only in consequence of the different environmental contingencies they may encounter. In the case of the metazoa, where a single organic whole with its parts in certain determinate hierarchical relations results from division, we again have the two possibilities of equal or unequal division. If the divisions are always equal (in the sense defined above) in this case we could only, it seems, interpret any differences that might later manifest themselves between the cells by supposing that it resulted from differences in their mutual relations in the organic "spatial" hierarchy. When we are considering the metazoa there are two interpenetrating hierarchies involved: (1) that generated by the process of cell-division, call it the "division hierarchy"; and (2) that resulting from the fact that the members of this hierarchy are related by yet another relation in addition to the one which constitutes the R_H relation in the division hierarchy. This relation is that complex multiple relation between the parts in virtue of which they *are* parts and not independent entities. This seems to be what people mean by the "organic relation," and is simply the relation of "being a part in an organic spatial hierarchy". A given individual also occupies a determinate position in a genetic hierarchy.

"Cells" can be classified in various ways, depending on the kinds of difference between them. First there is the kind of difference between say, a smooth muscle cell of a monkey, and a smooth muscle cell of a man, and secondly, there is the kind of difference between a smooth muscle cell of a man and a gland cell of a man. The first difference is one which does not "develop" but merely persists. It may be called a genetic difference, and it is this mode of classification of cells which is of interest to genetics. But genetics as an

experimental science cannot explain how the monkey-cells came to be different from the man-cells, since this was accomplished through a process which occurred in the remote past. It can only investigate such differences as they are now, not how they came to be. But the second kind of difference is one which develops and is the concern of the embryologist. For there was a time in the history of a given man when he had no smooth muscle cells and no gland cells. From the embryologist's standpoint, therefore, we can classify cells according to the determinate place they occupy in the division hierarchy. If we follow this method we see that the cells belonging to the highest levels are very similar to one another, and we call them embryonic cells, whereas the cells belonging to the lower levels, which are also later and belong to later temporal slices of the individual history, are very different from one another. The cells of these lowest or later levels appear to be divisible into three classes: (1) tissue cells; (2) cells which we may call "persistent embryonic cells," which are concerned in restitutive processes; and (3) germ-cells. Now tissue cells are distinguished from other cells by possessing cell-parts which have *never before been present* in higher or earlier levels of the particular hierarchy in question, although they will usually have been present in previous members of the *genetic* hierarchy. Thus one of the problems of embryology seems to be to explain how these tissue-cell-parts (e.g., myofibrillae, haemoglobin, secretion-granules, etc.) come to be developed in the cells, how it is that certain parts appear in some cells, and others in other cells, and how it is that they appear *when* they do.

Something must be said at this point about the term "differentiation." Under this term two quite distinct processes

appear to have been confused. By *differentiation* I shall mean simply a process through which two (or more) different parts come into being by the separation unequally between them of something previously present in *one* part (or whole). For example, it is by a process of differentiation in this definite but restricted sense that the cells of the animal pole of a frog's egg come to be different from those of the vegetative pole with respect to their yolk content. But there is another process by which parts may come to be different, namely when parts appear which were not previously present as such at all. Of this we have an example in the process already mentioned whereby cell-parts not previously present make their appearance in cells. I shall call such processes processes of *elaboration*, not differentiation.

It does not seem to me to be correct to define the "prospective potency" of a cell in the way Driesch (3) does as "the *possible* fate of a certain cell, i.e., the totality of possible characters of the adult into which this cell may develop." Because, in the first place, as will be seen below, cells do not develop into characters *at all*, and in the second place because only embryonic cells when they undergo their histological elaboration relatively late in development *can* be said to *develop*, and then it is actually only certain cell-parts that develop. Cells of earlier levels of the division hierarchy do not develop at all, they merely *divide*; that, and that alone, is their "fate".

We have so far considered only two embryological processes: cell-division, or the elaboration of non-cellular parts, and histological elaboration, or the elaboration of cell-parts. That the former is a process of elaboration becomes clear when we recall that the fertilized ovum has no parts characterized as cells, but only cell-parts, and that after cleavage there is a new level in the spatial hierarchy con-

stituted of cells as parts standing in certain determinate relations to one another. It seems clear from modern genetical studies that the cells belonging to a given race will only be capable of a certain restricted number of cell-part elaborations and it is not at all difficult to understand that an important rôle in this latter process will be played by the hypothetical "genes" required by geneticists, and regarded by them as *nuclear* cell-parts. These of course do not "develop" but only persist, except in so far as mutation occurs. It would be more correct to say that their *properties* persist. If all *nuclear* divisions are equal (in the sense defined) then, in so far as histological or cell-part elaborations depend upon the nucleus, *every* non-cellular part (in a suitable temporal part of the division hierarchy) will theoretically be capable of undergoing any of the histological elaborations of which the race is capable, unless the latter is heterozygous, in which case the cells of a given individual will be capable of only certain of the possible histological elaborations.

But, at least in the higher metazoa, there is another process of elaboration not yet considered, namely the elaboration of *cellular* parts. It will be seen below that it is this developmental process which presents perhaps the greatest difficulties. But before we can proceed further in this direction we must consider the causal postulate a little, and also devote some attention to the different kinds of "properties" and how they may be affected by the kinds of relations met with in organisms. This is of the greatest importance for the interpretation of the data of modern experimental embryology.

IV

The incautious use of the notion of causation, in accordance with the wholly uncritical practice of common sense, has

led to some appalling muddles in the discussion of genetical and embryological topics. Some biologists still seem to believe that a "character" can be "solely due to" or "caused by" either a "gene" or "genetic factor" alone, or by an "environmental stimulus" alone, as though "cause" and "effect" were isolated entities standing in a two-termed relation to one another and were completely indifferent to anything else in the world. A very little reflection should suffice to dispel this illusion. Others make some improvement upon this by saying that a given character is partly dependent upon genetic factors, and partly upon environmental factors. But this too cannot be correct if by genetic factors is meant parts of chromosomes, because no organism consists simply of a mass of chromosomes, and you cannot ignore the rest of the organism without further ado. The notions of "stimulus" and "response" are also often used very loosely in this connexion with unfortunate consequences. Among Schaxel's *Abhandlungen* a useful discussion of the use of the notion of stimulus has been contributed by P. Jensen (7). The following remarks about the causal postulate are chiefly confined to the requirements of the present paper.

In any causal investigation we always seem to have two "occasions" or "situations" which are *compared*. An occasion contains three principal constituents: (1) an organism, or part of an organism; (2) an environment; and (3) an observer. Or, we may have only one occasion containing two organisms in the same environment. Some simple examples will be helpful. Consider an occasion containing an organism, an observer and some stimulus, i.e., some environmental change. Suppose the organism gives the response *r*. On a later occasion containing a later temporal part of the same organism the same stimulus is presented. If the same

response is observed we say, in accordance with the causal postulate, that the organism has not changed (with respect to the process in question) since the first occasion. If we note a different response *r'* we say the organism *has* changed, it is a different organism, and it is because of this difference that the response *r'* differs from *r*, although this difference may not be observed but is hypothetical. Suppose now we take a number of fertilized eggs from a certain fish and divide them into two batches: one batch (a) is placed in normal sea-water, the other (b) is placed in water containing some abnormal constituent. If the embryos of (b) all exhibit some definite difference (the same in each embryo) from those in batch (a) we say that this difference is "due to" the abnormal constituent of the environment of (b), or, more correctly, it is causally correlated with the difference between the two environments. If we say that the abnormal constituent *caused* the observed abnormality all we are entitled to mean is that it was one element in a complex which is essential to the result observed. Finally, suppose we have two rabbits—one white and one black—born in one litter. Then we say that this difference was correlated either with a difference between the intrauterine conditions of the two embryos, or (which would be considered more probable) with some difference which was present *throughout* the development of both, i.e., a genetic difference.

Thus in all three cases we have comparison. If we observe a *difference* between the organisms concerned we assume either that the observed difference is correlated with some environmental *difference*, or that it is correlated with a previously existing, but perhaps unobserved, *difference* between the organisms concerned. We always believe that if any change occurs this is because something has happened in the

environment, or because a change has been going on unobserved in the organism. We can express all this in a simple symbolism:

- (1) $D(A, B).C.D(O_A, O_B)$ or $D(E_A, E_B)$
 (2) $D(A, B).C.D(O_A, O_B)$ and $D(E_A, E_B)$

These formulae are sufficiently obvious. "D" simply means "the difference between" whatever follows in brackets, and "C" means "is causally correlated with" what follows it. "A" and "B" are the two occasions (or two organisms in one occasion). "O" stands for organism and "E" for environment. We also require a third formula for cases in which the *relations* are different in the two occasions:

- (3) $D(A, B).C.D(R_A, R_B)$

Suppose in two occasions I have a lighted candle and a piece of sealing wax. In "A" these two constituents are six feet apart, in "B" the wax is in the flame. In the former case the wax is solid, in the latter it is melted. The other correlated difference is then the difference between the relations of the two constituents in the two occasions. The same would hold in embryological situations in which so-called "totipotent parts" are transplanted to different situations. It may be noted in passing that because we find a second pair it does not follow that this *is* causally correlated with the first.

We must turn now to properties. I shall use the term in a wide sense to include both perceptible characters, e.g., coat color, which may characterize an organism during a considerable period of its history, and also for a specific change which an organism (or part) may exhibit when it enters as a term in a specific causal relation. The most important point which requires explanation from the standpoint of the "concept of organism" is

the difference between what will be called "intrinsic" and "relational" properties. In natural science all causal properties are relational properties in the wide sense, but in considering organic wholes or parts it is necessary to distinguish between *viable* relations, and *lethal* relations, i.e., between those in which the organism (or part) lives and those in which it dies. Now by *intrinsic* properties I mean those which an organism or part exhibits in *all viable* relations, and by *relational* properties I mean those properties a *part* exhibits only in certain *organic* relations. And among intrinsic properties it will be necessary to distinguish between *original* and *acquired* intrinsic properties. Thus in a certain relation a part may acquire a property which persists even out of the relation. This would be an acquired property—acquired relationally but becoming intrinsic. This can be illustrated by analogy with "members" of a "social hierarchy." Consider an Englishman born in England. He will have certain intrinsic properties which he exhibits in all viable relations in common with all men, e.g. breathing, eating, etc. But he will also acquire certain relational properties which depend on the "specific hierarchy" to which he belongs. He will, for example, acquire the relational property of speaking English, but if in early childhood he had been "transplanted" to another "social hierarchy," e.g., to Germany, he would have acquired the different relational property of speaking German. He may also take to the sea and acquire the relational property of being steward on board ship. If he is cast upon a desert island he loses this and other relational properties and reverts to a more generalized type in which perhaps he exhibits chiefly his original intrinsic properties. Now precisely the same thing is true of the members of the various levels

in the organic hierarchy constituted by the single individual organism. Robinson Crusoe on his island is paralleled by the isolated cell in tissue culture. The important point is that the relational properties of parts depend upon their specific relations in the hierarchy to which they belong.

Now it may be the case that *all* specific histological elaborations are relational properties in the above sense, but that all the cells belonging to a given homozygous race have identical original *intrinsic* properties. But we must pause to consider certain complications. The intrinsic properties of a cell may depend upon both its cytoplasm *and* its nucleus. If two cells, which are assumed to have "equal" nuclei (in the sense defined) behave differently in the same environment, we should say (in accordance with the causal postulate) that they differed intrinsically in their cytoplasm, since their relations are supposed to be the same. But that intrinsic cytoplasmic difference may have been acquired in consequence of relational differences during development, and would therefore be an acquired relational property. But since it now persists in spite of changed relations (since by hypothesis both cells are in the same environment now) we should have to call it an acquired intrinsic property. We seem to have an example of this in the cardiac muscle fibres. These exhibit the elaboration of the rhythmical contractile property in the course of development and this (on the hypothesis under consideration) will be a relational property. But it may persist for years in tissue culture. Hence it is an acquired intrinsic property which is not lost in viable relations even if the part is removed from its place in the individual hierarchy.

Thus it is possible to conceive that throughout the four-dimensional divi-

sion hierarchy the nuclei are "equal" (i.e., that all nuclear divisions are purely quantitative, except of course the meiotic ones) and that differences between cells (as far as tissue-cells are concerned) are always a consequence of acquired relational properties (which may become intrinsic). Differences between cells may arise either by differentiation or elaboration, and it is in connection with the latter process that relations and relational differences are so important. If we make these assumptions (which seem to have a good deal of empirical evidence in their favor) we shall be able to interpret and state in precise terms many of the curious results which have emerged from transplantation experiments. Some such view as this seems to me to be forced upon us. It will be seen, after a little reflection, that relational properties are of immense importance in an organism, and that far too little attention has been paid to them. It is here that the machine analogy has put us on a wrong scent. There is not discernible in machines a level constituted of parts which are such that the level is homogeneous with respect to the type of organization of those parts, as is the case with the cell-level, and in which the parts can become different in accordance with their relations in the hierarchy. Moreover the *maintenance* as well as the elaboration of specific cell-parts is in some cases dependent on their relations, as is clearly seen in some tissue-culture experiments. In other words the parts in an organic hierarchy are internally related, whereas in a machine these relations are external or non-constitutive relations. How long are we to persist in refusing to look sheer hard facts in the face, merely in the interests of a seventeenth-century analogy which by now may well have outgrown its usefulness? Sooner or later biology will have to take account of them

if there is to be any theoretical biology, as contrasted with a "medley of *ad hoc* hypotheses."

Another important point came to light in our consideration of hierarchical order in the abstract. It was noted that a given member can be regarded from three points of view, namely from that of (1) its membership of a level, i.e. its R_L relations; (2) its entering into the constitution of a member of the next highest level, i.e., its R_H and R_A relations; and (3) its analysis into an assemblage of members of a lower level in their R_A relations. Now it has been the custom to regard a given organic part almost exclusively from the third point of view, namely from that of its analysis into parts and their properties. But clearly in an organic hierarchy R_H relations will be of equal importance, otherwise its parts would not be different in isolation from what they are in their place in the hierarchy. In other words they would be externally related to one another, like the parts of a machine, which does not seem to be the case. It is for this reason that E. B. Wilson seems to me to be in error when he writes (16), regarding the "organization" of the germ-cells which he says "determines" the "particular course" of development:

Nevertheless the only available path towards its exploration lies in the mechanistic assumption that somehow the organization of the germ-cell must be traceable to the physico-chemical properties of its component substances and the specific configurations which they may assume.

How will this be the case if the fertilized ovum is an organic hierarchy with levels *above* the chemical level? We should expect the properties of the members of the chemical levels to depend upon their R_H relations to members of *higher* levels. In a recent lecture in London on the results of micro-injection experiments it was stated that proteins are not present as such

in certain living cells. If this is the case it is precisely what we should expect from the organic standpoint. Also it always seems to me to be dangerous to use the word *must* in natural science. That is an expression which may safely be left to fundamentalists and their friends. Let us set them a good example by saying "may" instead of "must," and "probable" instead of "certain," which is all we are usually entitled to say.

Another instance of the neglect of the implications of the concept of organism in the past is furnished by a recent paper by J. Gray (5), in which he discusses the methodological problems involved in the interpretation of growth curves. In his summary he writes:

Graphic treatment of the data underlying a typical growth curve is liable to produce errors of considerable magnitude, and often tends to confuse the facts. The units which compose a metazoan's body form a very heterogeneous system, in which the rate of growth of one organ is dependent on that of others. It is, therefore, intrinsically improbable that the behavior of such a system should conform to that of a simple chemical system in which the variables are few in number and capable of accurate analysis. The conception of growth as a simple physico-chemical process should not be accepted in the absence of a very rigid and direct proof; at present, it rests on the results of a process of graphic analysis which is often, if not always, of a relatively inaccurate nature.

This clearly represents the first gleams of the dawn of the concept of organism in one consciousness, but a little reflection would have given us even more than this without huge chunks of algebra and pages of graphs. Who but a very learned man would dream of conceiving the growth of a metazoan as a "simple physico-chemical process"? And yet biologists no more ask for a "proof" of this than fundamentalists ask for a proof of the infallibility of the Scriptures. Surely this is a shining example of what C. D. Broad (2) calls a "silly theory" in the sense of one "which

may be held at the time one is writing professionally, but which only an inmate of a lunatic asylum would think of carrying into daily life." Now such silly theories are quite indispensable for scientific progress, but it is not only fatal to carry them into daily life (as people frequently do), it is also fatal to take them too seriously in science, lest they harden into dogmas which obscure our intellectual vision, as this one seems to have done. The whole difficulty in relation to these problems rests very largely, I think, on the deep-seated belief that only the ultimate scientific objects into which an organism is believed to be analysable are "really real" (e.g., electrons) and that everything else is "mere appearance" and can be safely neglected. But this is a big subject and here I can only refer the reader to the book by Whitehead (14) already mentioned. This too is a meta-physical legacy from an earlier age.

V

Returning now to the particular problems of genetics and embryology we first have to ask: What does a geneticist mean by a "character"? Consider, for example, a patch of black on some animal's skin: does he mean by the character the very black patch which we see, or does he perhaps mean a vast number of little pigment granules in the skin? If the latter is meant then he is not talking about a character at all but about certain *parts*, and these parts may differ in their properties (characters) from corresponding parts in a related animal. If you try to avoid this by saying that these granules are analysable into sub-parts which differ only in their relations you still do not escape from the antithesis between parts and their characters or properties. Because your ultimate parts will not be *mere parts*, i.e., spatio-temporal entities, but

will be distinguished in some way from other spatio-temporal entities by characters or properties of some sort, otherwise the world would consist of a single uniform spatio-temporal entity with no "things" in it at all. Let us say, then, that *correlated* with the black patch which we see there are also, in certain cells of the skin, little pigment granules which differ in their properties from those in the skin-cells of a related animal which has, say, a *yellow* patch correlated with its pigment granules. Let us try to conceive how this is to be interpreted embryologically and genetically. We go back to the fertilized ova from which the two hierarchies were generated by division. In accordance with the chromosome hypothesis we assume that the chromosomes of these two ova differ from one another in some respect, and that with this the difference between the properties of the two kinds of skin-cell granules is correlated. Cleavage now begins, and we assume that the chromosomes are divided equally at each division. This continues until we have a quantity of cells *all* of which, so far as the nucleus is concerned, are capable of elaborating a certain sort (but only *one* sort in *each* whole embryo, i.e., according to the "genetic" classification of its cells) of pigment granule. But towards the end of development, when these granules begin to make their appearance, they do not *appear* in *all* the cells but only in *some* cells. Consequently (if we are to apply the causal postulate) we shall have to appeal to something else to "make the difference" (as we say in everyday life when we are not being "silly"). We seem to have but two alternatives (or a combination of both): either it is because the *relations* of the skin cells are different from those of the other non-cellular parts (in accordance with our third causal formula); or because the

cytoplasm is different in these cells. There are facts which would justify the assumption that *if* the difference is to be traceable to cytoplasmic differences these can themselves only be relational (not original), i.e., acquired through relational differences earlier in ontogeny. Thus the hypothetical animal we are considering might be one of those in which, at a suitable stage, it would be possible to transplant cells from, say, the black to the yellow specimen, and they might then develop, not into skin cells but into neural-tube cells with no pigment granules in them at all. As we are trying to consider a purely hypothetical general case we shall make the assumption that the differences between the pigment cells and the remaining cells of the body are *not* dependent upon original cytoplasmic differences but only on relational differences (including differences resulting perhaps from relations of earlier periods). In other words the property of developing pigment granules (as contrasted say with myofibrillae) is a *relational* property. But the property of developing "black" pigment granules in the one case, and "yellow" ones in the other, is clearly an original *intrinsic* property, and distinguishes *all* the cells of the one race from those of the other. It is these properties with which geneticists deal. This enables us to understand how it might happen (as has been shown to happen in some cases) that cells from the "black" specimen from a part which would not ordinarily exhibit skin cells, might be transplanted to a "skinny" situation on the "yellow" embryo, and would there behave "ortsgemäss" but would still elaborate not "yellow" but "*black*" granules. Transplanted parts retain their "species specificity." The skinny situation furnishes the particular *organic relations* requisite for the development of *granules* (as contrasted with other possible

histological elaborations), but since the particular color correlated with the granules depends upon the intrinsic properties, not on the relational properties (in the sense here used) of the cells, the particular granules in this case will still be "black."

So far so good. We have seen how it is that all the cells may have a complete stock of genes, and how all of the genes *may* be involved in the elaboration of what is necessary for the manifestation of a single character, *provided* we are willing to recognize the difference between intrinsic and relational properties of non-cellular parts, and the existence and importance of internal relations in an organic hierarchy. Such possibilities were closed to Weismann because he assumed that the properties of a cell (non-cellular part) depend *only* on its nucleus (at least during development) and thus completely ignored the mutual internal relations between parts. He was therefore driven to assume also that "there are material particles in the germ each of which is to be regarded as the primary *Anlage* of one portion of the organism," and that "the chromatin which controls the properties of cells must be different in each kind of cell." (Thus chromatin takes the place of Descartes' God as the "controlling" mechanic). In conformity with the age in which he lived Weismann also asserted that these assumptions *must* be accepted as correct *for all time to come!* (12). Dogmatism is a deep-seated vice of human nature not confined to theologians (i.e., not a specific relational property!).

But now comes the difficulty. We have all along been taking these specific organic relations in the hierarchy for granted, whereas these relations themselves develop or come into being and this itself constitutes one of the problems of embryology. Development does not consist simply in a process of cell-division followed by one of

histological elaboration. Moreover, we started with a black patch but we have been considering only its blackness and forgetting its shape, size and (perhaps) symmetrical relations to the whole. These are also characters. In considering the blackness of the patch we could concentrate on one process, namely the elaboration of intra-cellular pigment granules with certain properties (i.e., the property of having a *black* color correlated with them for an observer). This might have been the case even although only one cell had been involved. But our patch may involve thousands of cells, and consequently in dealing with its size, shape, and relation to the whole we cannot confine ourselves to what is happening in individual cells. All this means that there is another developmental process to be considered, namely the elaboration of *cellular* parts, of parts, that is to say, which are analysable into cells in certain determinate relations, and which thus constitute parts belonging to a level above that of the cells. It should be remembered that it is upon these parts and their relations (in so far as they differ in different districts in the whole) that we have been driven to place the "responsibility" for the differences in the histological elaborations of the various non-cellular parts which (in their relations) constitute them.

We must go back again to the beginning of development. Conceive an ovum which undergoes a perfectly equal holoblastic cleavage, resulting in a blastula with a perfectly uniform wall consisting of cells all having precisely the same original *intrinsic* properties. This would be an "harmonious equipotential system." Let it undergo gastrulation. Now the causal postulate requires that there should be some difference between the part of the gastrula wall which is invaginated and the rest—either in the organism or

in the environment. But by hypothesis it seems that there is no difference in these two parts of the organism, and if we are to rely on the environment then gastrulation would depend (and which particular part is invaginated would depend) on a mere environmental contingency. And this does not seem to be the case. But, it will be said, it is useless to consider such a hypothetical case because no such thing ever happens—the ovum always exhibits some polarity which, in the blastula, is differentiated among the cells of the two poles, and it is this which is responsible for the differences in their behavior. Very well then, let there be some such difference, say of size, as seems to be the case in *Amphioxus*, and let this be a sufficient difference to account for gastrulation, as Assheton tried to show (1). This would be a case of differentiation by unequal cytoplasmic division with respect to volume. But this will only help us over one stile and there are very many to cross. Having got our gastrula we now have two cellular parts established: ectoderm and endoderm. We thus have some scope for different relations in the hierarchy. But is this sufficient? What is to "make the difference" (as common-sense folk always say) between right and left halves, dorsal and ventral surfaces? Moreover, we next require differences between the different parts of the archenteric roof to enable us to understand how it is that some become mesodermal pouches, and one becomes notochordal tissue. We can hardly go back to a cytoplasmic "preformation" for these latter differences, because it seems clear from various experiments that they involve relational properties and depend primarily on the blastoporic lip. If we are to assume that some minute part of the egg-cytoplasm is destined to form the organizer how will this enable

us to understand the *differences* in the parts of the region it organizes? And even this will not take us very far. As development proceeds more and more cellular parts are elaborated, and if these are all to be referred back to the egg-cytoplasm the latter will become, it seems, intolerably overcrowded. Are all the cellular parts of a man represented in the minute amount of cytoplasm of the human ovum? What, then, shall we say in those cases in which it is possible to chip off pieces of cytoplasm in any direction without preventing the elaboration of cellular parts? How shall we interpret "identical" twins? Does each blastomere possess a complete preformation? It seems clear that a cytoplasmic preformation is as difficult to believe in as Weismann's nuclear one.

Let us then review the possibilities regarding the modes of elaboration of cellular parts as they appear to our present ways of thinking. We seem driven to choose between: (1) a nuclear preformation; (2) a cytoplasmic preformation; (3) environmental differences during the ontogenetic period; (4) appealing to a transcendent "principle"; (5) rejecting the causal postulate. Of these (1) and (3) seem to me to be excluded by modern experimental data as decisively as anything can be excluded by experiment. I can see no possibility of help from (4). This leaves us with (2) and (5), which are not so simple and clear cut as might be supposed at first sight. Even Driesch shrinks from rejecting the causal postulate, at least in the form of the "principle of sufficient reason." And to suggest such a thing in scientific circles is like uttering one of the nine unprintable Anglo-Saxon monosyllables at a polite tea-party. But nevertheless there is still scope for plenty of discussion regarding the use of the causal postulate in embryology. To

do this adequately here would carry us far beyond the confines of a single paper. It should, however, be understood that *if* there are equipotential systems, and *if* we are bound by the principle of sufficient reason, then it would absolutely follow that there were some such entities as Driesch's entelechies. I doubt whether the majority of embryologists have fully realized this. But to explain this fully would also take up too much space. All that seems to remain is some kind or degree of "cytoplasmic preformation." Would it be possible to appeal to just enough cytoplasmic preformation to give us our main axes and the primary germ-layers, and could we from thence forwards appeal on a large scale to relational properties? At first the latter would be involved in the blocking out of the main districts during the earlier periods. When these are "set" in accordance with relational properties they behave "*herkunftsgemäss*" on transplantation; hence their morphogenetic properties are now "acquired intrinsic" although *relationally* acquired, as shown by the totally different result of an earlier transplantation. But within each of these main "blocks" there will presumably be sub-parts which undergo elaboration in accordance with relational properties, until finally we reach histological elaboration as already explained. Moreover this "minimum" cytoplasmic preformation to which we are appealing will itself be the outcome of intra-cellular elaboration in accordance with the ovarian relations furnished by the maternal parent. And this enables us to burden the chromosomes with no more than the duty of providing what is needful (whatever that may be) for the various possible histological elaborations of which a given race is capable. This is all that "genes" need to do apart, of course, from persisting and dividing.

This possibility, then, has its attractions. But will it square with "identical" twinning and with cutting and transplanting experiments? Does it put too much upon relational properties? These are questions requiring further thought and experiment. Experiments should be devised for testing relational properties in greater detail and with greater precision. Also it is very important to know whether there *really are* equipotential systems in the organic realm. A great deal hangs upon this. To sum up: the crucial problems of embryology seem to be those concerning the three principal modes of elaboration—of cellular, non-cellular and of cell-parts. And it seems perfectly clear that it is the *primary* duty of the embryologist to discover how to interpret the developmental process in terms of the intrinsic properties of the various "genetic types" of cells and the relational properties they exhibit in the several hierarchic organic relations which arise in the course of the elaboration of non-cellular parts, and which are accessible to our observation. And this primary objective is quite independent of any theoretical views we may hold regarding the ultimate "reducibility" of biological to other branches of natural knowledge. It is not the business of the biologist to lose his way in a fog of hypothetical imperceptibles. I agree with the physicist who wrote: "I have no doubt whatever that our ultimate aim must be to describe the sensible in terms of the sensible." If Lavoisier, at the foundation of chemistry, had proceeded on the

assumption that it was the business of chemistry to reduce itself to physics there would probably never have been any chemistry. The moral for biology is obvious. There is no short cut to biology if it cuts blindly across the observable facts of biological organization. Not to recognize this means tying biology down either to the "verification" of the metaphysics of Herbert Spencer, or, if it is only interpreted methodologically, to an extremely restricted circle of thought devised, in the first instance, on account of its value in a different sphere. This does not apply, of course, to genuine bio-physics and bio-chemistry in their own fields, but to vague speculations in other branches of biological inquiry which merely borrow their terminology and ape their manners.

The "concept of organism" seems to be forcing itself upon our attention from three directions: First, from that of embryology and physiology. The notion of a morphogenetic "field" in Gurwitsch (6) and Weiss (13) is highly symptomatic of this movement and deserves attention. Secondly, there is the *Gestalt-theorie* beginning in psychology and extending to physics (8). Thirdly, there are those philosophers of evolution—Hobhouse, Alexander, Lloyd Morgan, Smuts and Whitehead—all of whom employ the concept of organism in various ways and degrees not exclusively biological. Perhaps this concept will enable us to understand evolution. Has anyone observed a machine that was capable of evolution *without a mechanic*?

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HISTORICAL SURVEY OF THE DEVELOPMENT OF THE SYMPATHETIC NERVOUS SYSTEM

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INTRODUCTION

THE development of the sympathetic nervous system has been and still is one of the most discussed problems of vertebrate embryology. During the last sixty years the literature on this subject, representing the investigations of a very large number of workers, has become extremely extensive and it reveals no agreement concerning the most fundamental points of the question. The researches were carried on in all groups of vertebrates; the anatomical findings were corroborated by embryological observations; the experimental procedure was applied in various ways; still our knowledge concerning the origin and the development of the sympathetic nervous system is very incomplete and scattered.

It was our purpose to carry on new investigations in this field, mostly from the embryological standpoint, supporting the morphological observations by experimental demonstration.

The literature is always partly reviewed by the many investigators, but no complete survey is to be found. The anatomy, the physiology and the pathology of this system are extensively discussed in many publications, among which the outstanding are those by Langley, Langdon Brown, Guillaume and L. R. Müller. The embryological aspect is generally very briefly

summarized or overlooked; it may even seem extraordinary to have physiological or pathological discussions, classifications and theories without any serious knowledge of what the sympathetic nervous system is, where it comes from and how it develops. We believe that before presenting our original contribution to the problem, it might be useful to offer a complete review of the embryological facts hitherto described and to try to get out of it, impartially, a few positive problems to be studied in order to establish a definite theory about the development of the sympathetic nervous system. In making this review, we shall follow the chronological seriation, grouping however, the different publications of the most important investigators; we shall also group the most important data concerning the development of the chromaffin system.

The term "sympathetic nervous system" is used with many different meanings, giving rise to many misunderstandings; actually it has been replaced by Langley's denomination "autonomic nervous system" (involuntary nervous system of Gaskell, système nerveux organovégétatif of Guillaume, Lebensnervensystem of L. R. Müller). The autonomic nervous system includes the ortho- and the parasymphetic systems, as well as the intravisceral nervous structures.

Our review deals in fact with the autonomic nervous system of the trunk;

it represents all the embryological data concerning the thoracolumbar sympathetic chains and the visceral part of the vagus complex. A few references are given to the development of the head sympathetic nervous system. These will represent the actual state of that aspect of the question, and in them the complete bibliography will be found. We shall not consider the purely anatomical facts nor refer to the physiological experiments unless they offer a striking confirmation or support to the embryological observations; neither shall we report any phylogenetic theory elaborated in comparing the autonomic nervous system and the nervous organization found in invertebrates.

This survey is to be the introduction to a series of studies concerning the development of the autonomic nervous system; as such, and in order to avoid frequent repetitions, we shall refer to it as a bibliography. The recent book of A. Kuntz on the autonomic nervous system appeared too late for critical review in this paper.

REVIEW OF THE LITERATURE

Histogenesis of the Autonomic Nervous System

Remak in 1847 was the first scientist interested in the anatomy and the embryology of the sympathetic system. He suggested that the primordia of the sympathetic ganglia were formed by proliferation of mesodermic elements at the point where the communicating rami arise from the spinal nerves.

The first appearance of these anlagen is seen in the chick embryo at the end of the fourth day of incubation; during the sixth day a big nerve trunk, called since then the nerve of Remak, develops all along the intestine. This nerve, also probably mesodermal in origin, was described as entirely independent of the

sympathetic cords. Nearly thirty years later Goette confirmed that conception without bringing in any new observations.

The first important embryological contribution to this subject was made by Balfour ('78) in a series of papers dealing with the anatomy and the development of the elasmobranch fishes. He showed the first trace of the sympathetic system arising as short branches from the spinal nerves, directed toward the median line of the body and terminating in small irregular cellular masses lying dorsal to the cardinal veins; these cellular clusters always retain their connection with their respective mixed spinal nerve by a small fibrous branch which will become the communicating ramus. In the young stages there are no apparent intersegmental commissures, the sympathetic cords being secondary structures; the most anterior sympathetic ganglion is in the heart region close to the end of the intestinal branch of the vagus; the last one being at the very end of the abdominal cavity. From the cellular prevertebral heaps, fibrocellular branches may be followed to the intestinal tract; he suggests the schematic formula that each spinal nerve divides into three branches: a dorsal, a ventral and an intestinal one. One year later Schenk and Birdsall applied the ideas of Balfour to the upper classes of vertebrates. In a chick embryo of five days incubation, as well as in a human embryo measuring twenty-two millimeters, the sympathetic primordia are not yet developed; but from the distal end of the spinal ganglia arise groups of cells migrating along the dorsal roots and in the mixed spinal nerves. These migrating elements, keeping their connection with the spinal nerve, become the anlagen of the sympathetic system. From these prevertebral ganglia arise new branches contributing to the formation of the prevertebral

plexuses and of the visceral plexuses; the Auerbach plexus is directly connected with the sympathetic cords.

In 1886, Onodi published a very extensive piece of work dealing with the development of the sympathetic system in the entire vertebrate series, showing clearly that the sympathetic trunks and the prevertebral plexuses arise from the central nervous system, more exactly from the spinal ganglia. The migration of cells from the distal end of these ganglia is due to the pressure exerted by the newly formed cells within the ganglion; it is thus a purely passive migration. He was unable to detect the origin of the peripheral sympathetic plexuses and suggests their mesodermal origin for lack of other evidence. In *Scyllium* the first anlagen of the sympathetic ganglia are seen as triangular thickenings of the ventral pole of the spinal ganglion in every trunk segment; the cells forming those thickenings result from mitotic processes in the spinal ganglion cells, and show in themselves a very marked karyokinetic activity, the result of which is their migration toward the dorsal and lateral aspects of the aorta and along the small vessels running in the root of the mesentery. The sympathetic ganglia so formed are then connected with the spinal ganglia by small communicating rami; later on they send commissural branches to each other, thus forming the sympathetic chains. Van Wijhe ('89) briefly refers to the sympathetic system in describing an embryo of *Pristiurus* at the stage of 84 somites; he shows that each segment of the suprarenal organ with its corresponding sympathetic ganglion is derived from a cellular proliferation in the spinal nerves, the proliferating and migrating cells remaining always connected with the spinal nerves by fine nerve fibers.

Paterson ('90) believed that the sym-

pathetic structures arise as a continuous, non-segmented cellular cord, the cells of which are derived from the mesodermal tissue; the segmentation of this chain is only secondary to the establishment of late connections with the series of spinal nerves and to the relations with the vertebral column. W. His ('79) in a 7 mm. long human embryo did not find any sympathetic anlagen, while the spinal ganglia were well developed and the mixed nerves formed; immediately after this stage he sees short visceral branches arising from the spinal nerves a short distance beyond the junction of the anterior and posterior roots and growing toward the aorta. These branches are purely fibrillar at this time; cells showing clearly their nervous nature migrate later apparently from the spinal ganglia; from the retroaortic sympathetic ganglia nerve trunks grow out toward the visceral organs and constitute the peripheral sympathetic plexuses.

His, Jr., and Romberg ('90) showed that the sympathetic cells were not pushed out of the spinal ganglia or later from the prevertebral sympathetic ganglia as a result of increasing pressure behind them through a rapid cellular migration, but that they were actively migrating into the surrounding tissue; the cells are at this stage apolar, and there is no indication at all of any deformation that would be the result of a passive pushing out by pressure. From the ganglia of the sympathetic cord the cellular elements wander out ventrally to give rise to the coeliac and other peripheral ganglionic masses. This peripheral migration is clearly described for the ganglia of the cardiac plexus in fishes, amphibians, birds and man; it appears to occur along the veins in fishes and amphibians, along the arteries in birds and mammals.

Golowine ('90) studied the development of the ganglionic system in chick

embryos; his work deals mainly with the relations existing between the nervous system and the sense organs. He considers the neural crest as originating from the ectoderm in common with the sense organs, independently of the nervous system. The sympathetic system originates from the ventral part of the spinal ganglia, when these are not yet fully differentiated; the anterior roots are at first cellular and appear only when the sympathetic ganglia are becoming independent of the spinal ganglia.

Goldberg ('91) verified the descriptions of His, Jr., without bringing in any new facts.

In a four day chick embryo, His, Jr., ('92-'93) showed that the clusters of apolar sympathetic cells found in the mesenchyme between the aorta and the point of junction of the spinal roots are evidently derived by migration from the spinal ganglia. In a later paper published in 1897 he described the succession of two sympathetic chains; the first one appears at the end of the third day of incubation and forms a continuous ganglionic cord on each side of the aorta, an abdominal plexus and a pelvic cord. That chain becomes less and less distinct and has entirely disappeared during the eighth day; at this moment the ventral pole of the spinal ganglia shows the wandering out of a new generation of migrating elements contributing to the formation of the secondary and permanent prevertebral chains. This description of His, Jr., is the first complete study of the development of the sympathetic system, based on a series of embryonic stages; it represents the most careful piece of work in this field hitherto published and its conclusions appear perfectly justified.

In 1898 Fusari studied the development of the sympathetic nervous system and of the adrenals in chick and mammals. In

the chick embryos he describes the first anlagen of the sympathetic trunks around the stage of sixty hours; at that stage the spinal ganglia are developing, but their peripheral branches do not yet reach the ventral roots and are far away from the sympathetic anlagen. A continuous longitudinal sympathetic chain is constituted on either side of the aorta before any connection can be traced between it and the spinal roots either ventral or dorsal; the communicating rami appear only later by the growth of fibers from the sympathetic ganglionic masses. The intestinal nerve of Remak seems to be at first independent of the sympathetic anlagen, with which it later acquires connections. The adrenals are formed by the intermingling of true mesodermal elements with others derived from the sympathetic anlagen. The sympathetic system seems to be derived from the elements of the protovertebrae and is not genetically related to any part of the central nervous system.

In a short paper published in 1894, G. Mazzarelli dealt with the origin of the sympathetic in various vertebrates, including selachians, amphibians, reptiles and birds. In *Passer* the youngest stage, for which no exact age or measurement is given, shows bands of isolated cells migrating from the ganglion crest region toward the lateral aspect of the aorta; these cells are doubtless neuroblasts. In a later stage this migrating band divides transversally into a dorsal part giving rise to the spinal ganglion and a ventral one representing the anlage of a sympathetic ganglion. This second stage described by Mazzarelli seems to correspond to the youngest stage studied by Paterson and Fusari, who in that way misunderstood the primary origin of the sympathetic ganglia. Mazzarelli's conclusions are also concerned with other groups of verte-

brates, though the migration is much less important in birds than in selachians and is still less marked in mammals.

In a series of papers, Dogiel ('95-'96) described the microscopic anatomy of the sympathetic ganglion, as well in the pre-vertebral chains as in the visceral organs. A very important result of his observations is the demonstration of two types of nerve cells in the intestinal plexuses. The first type is identical with the motor elements of the cerebrospinal nervous system, with short, very richly ramified dendrites and one long neurite passing more or less deeply into the musculature. The second type represents cells with from two to ten dendrites coming from the glandular and epithelial structures and one neurite going toward the type I cells; the dendrites are supposed to be receptors of stimuli which are conveyed by the neurite to the motor cells. Both cellular types are to be considered as sympathetic in origin, although Dogiel did not try to base his assumption on embryological studies.

Kölliker ('94) verified the origin of the sympathetic system as a result of the migration of cells out of the spinal ganglion and identified all the peripheral plexuses as sympathetic derivatives. The same year, Rabl described the first anlagen of the sympathetic system in *Pristiurus* at the stage of seventy-four somites as a thickening along the spinal nerve, due to an elongation of the corresponding spinal ganglion.

In 1900 Hoffman studying the development of the sympathetic system in selachians found its first appearance in a 15 mm. embryo of *Acanthias vulgaris* as cellular heaps to which the contribution of the spinal ganglion seems much greater than that of the motor roots. These cellular masses increase in size and differentiate into a medial part, which becomes the sympathetic ganglion, and into a lateral

one mostly fibrillar, which gives rise to the ramus communicans. The sympathetic chains show segmental ganglia except for the first three cervical segments, the first trunk ganglion being connected with the fourth cervical nerve; the sympathetic ganglia corresponding to the four or five following spiral ganglia fuse to give rise to the superior cervical ganglion. Taking into account the fact that the sympathetic trunks appear only after the constitution of the mixed spinal nerves and arise near the junction of both roots, Hoffman concluded the necessity of that junction for the development of the sympathetic anlagen. In the head, where such junctions do not occur, no sympathetic ganglia are to be found except at the connection between the ophthalmic nerve and the oculomotor nerve, the ciliary ganglion being the result of this junction. In the idea of Hoffman, the ciliary ganglion is the only true sympathetic ganglion in the head. In 1902, studying the development of the sympathetic system in urodeles, he described the first sympathetic anlagen as being connected by narrow strands to the ventral roots as if the cellular migration of the sympathetic elements had been accomplished along the ventral roots.

O. Schultze ('94) in embryos of *Vespertilio* found the first trace of sympathetic elements as an unsegmented chain running in the corner between the aorta and the intersegmental arteries. The sympathetic elements there located seem to arise from a differentiation of mesoblastic elements, or more exactly, he found no reason to admit that they migrate from the spinal ganglia.

Onuf and Collins ('00-'02) published a very extensive piece of work about the central localization of the sympathetic nervous system with a critical review of its anatomy and physiology. This paper, frequently overlooked by later authors, is a

very important contribution to the problem of the sympathetic system and is one of the first experimental studies with an anatomical purpose. Before discussing these researches we want to say a few words about a very ingenious theory advanced by Jendrassik ('99). This investigator divides the sympathetic nervous system into the spinal and the vagus systems. The spinal system includes the ganglionated cords and the peripheral ganglia located near or in the different organs; the vagus system is represented by the vagus nerve. The vagus nerve should be considered as a purely sensory nerve, the motor fibers running with it belonging in fact to the neighboring nerves; the branches of the vagus nerve to the organs convey the sensory impulse to the jugular ganglion and to the medullae-oblongatae nucleus, from which fibers exclusively motor in function go to the spinal system.

This theory, however interesting it may be, is strongly contradicted by very positive observations of Langley ('03) and Kölliker ('94). These two authors proved that the sympathetic system contains at the same time centripetal and centrifugal fibers, and that in the centrifugal fibers some were motor and others inhibitory; the purely sensory function of the vagus is, therefore, to be discarded! However, nothing definite is yet known concerning the possible origin of the sensory sympathetic fibers nor their connection with the cerebrospinal system. Kölliker claims that all the sensory fibers of the sympathetic system originate from cells of the spinal ganglia in exactly the same way as do the sensory cerebrospinal fibers. Dogiel ('95) is inclined to assume the existence of specific sympathetic sensory fibers arising from the cells of the sympathetic ganglia or plexuses. Sala ('93) describes two

types of fibers in a sympathetic ganglion; the varicose fibers and the dividing fibers. The varicose fibers, presenting a tortuous course, remain in the ganglion itself without giving off any collateral branches and are to be considered as true sympathetic fibers originating from cells of the sympathetic ganglia; the dividing fibers send off numerous collaterals, the ramification of which forms the diffuse network of the ganglion. These only are derived from the cerebrospinal system. Gaskell ('86) noticed for the first time that while the communicating rami were composed of medullated fibers, the efferent rami of the sympathetic ganglia contained non-medullated ones; he was also the first to carry on a combined anatomophysiological experimentation on the visceral innervation of the crocodile. In the young crocodile the rami communicantes between the spinal nerves and the ganglionic chain are very short and the spinal ganglia are very near the corresponding sympathetic ganglia; in the tortoise the ramus communicans in the thoracic region springs directly out of the posterior root ganglion, while according to Giacomini in *Bufo* and *Bombinator* the two ganglia actually touch one another.

Gaskell cut the vagus nerve above the ganglion trunci vagi and stimulated the nerve at the peripheral cut end, obtaining a strong peristaltic contraction of the whole oesophagus and of the stomach; the same effect takes place when the stimulus is applied below the ganglion. After allowing degeneration, the stimulation above the ganglion does not produce the slightest effect on the oesophagus or the stomach; the same stimulation below the ganglion causes a marked contraction except in the cervical part of the oesophagus. These experiments prove that the fibers for the thoracic portion of the oesophagus

and for the stomach are interrupted by the cells of the nodosum ganglion while those for the cervical oesophagus are not.

In removing a few sympathetic ganglia without touching the spinal ganglia Onuf and Collins ('00) observed a degeneration of the cells of Clark's column and a degeneration of fiber bundles going from the posterior root to Clark's column; the fiber degeneration exists at the level of the sympathetic removal, while the cellular degeneration is only to be found a few segments higher. Thus the sensory fibers of the sympathetic system do not originate from spinal ganglion cells but from those in the sympathetic ganglia; the sensory fibers after having reached Clark's column make an ascending course to and around Clark's cells at a considerably higher level. The extirpation of both stellate ganglia produces atrophic changes in the lateral horns, both paracentral groups and both columns of Clark from that level down to the ninth dorsal segment; the downward extension may be due either to a descending extension of fibers in the spinal cord or in the sympathetic chain.

In 1905 Jones published a short paper on the development of the sympathetic nervous system in the toad. Although brief and rather incompletely worked out, it has the great interest of bringing forward important observations. Between the vagus ganglion and the second spinal nerve he describes at the 9 mm. stage sympathetic cells scattered in the mesoblast dorsolaterally to the aorta; these cells show a tendency to aggregate themselves in an irregular longitudinal cord, which becomes well defined at 12 mm., being followed continuously down to the sixth spinal nerve. At the level of the fourth spinal nerve exists an enlargement corresponding to the position of the adrenals. At 14 mm in length the rami communicantes can be seen as fibrous branches con-

necting the primarily isolated sympathetic clusters with the mixed spinal nerves; at 21 mm. there exists a very intimate connection between the vagus ganglion and the anterior end of the sympathetic chain.

Neumayer ('06) in *Lacerta* finds the first sympathetic anlagen in an embryo in which the auditory vesicle is not yet entirely separated from the ectoderm. On the medial side of the mixed spinal nerve, already fibrillar but still presenting numerous migrating cells, he describes a small fibrocellular branch directed medially and ventrally toward the aorta. Somewhat later the branch itself, purely fibrillar, becomes the communicating ramus, while its end is thickened in a cellular cluster, the primordium of the sympathetic ganglion. The sympathetic anlagen are to be considered as cellular buddings of the spinal nerves.

In an 11 mm. embryo of *Pristiurus*, the ganglia appear as small buds of the mixed spinal nerves, near the junction of the ventral and the dorsal roots; from those cellular heaps, small branches are growing along the mesial aspect of the mesonephros. Later on, the primordium of the sympathetic ganglion divides into a mesial portion, cellular, and a lateral one representing the communicating ramus; from the ganglion, a few fibrocellular branches extend in the mesentery and spread into the walls of the intestine. Fusari also studied the development of the sympathetic system in mammals and concluded that it is derived neither from the spinal ganglia nor from the neural tube, but is the result of a local differentiation of the elements of both roots, exactly in the same way as the spinal ganglion cells and the nerve fibers are derived from elements differentiating in situ.

In 1905 and 1907, Kohn studied the histogenesis of the sympathetic nervous system in mammals, especially in the rabbit;

this description might be taken as a model of embryological study of the sympathetic system. In eleven-day old embryos he does not find any trace of the sympathetic system. Six hours later he observes the first step in the migration of sympathetic elements. Their origin is altogether from the neural tube along the anterior roots and from the spinal ganglia. The emission of neurocytes from these two sources does not continue a long time, but numerous mitoses occur in them, resulting in the progressive multiplication of sympathetic elements. In eleven days and fifteen hours, the migrating neurocytes reach the lateral aspects of the aorta, and at this level they accumulate, forming small ganglia, very rapidly acquiring connections with each other and constituting an uninterrupted reticulum along the body of the embryo. In twelve days, the sympathetic system begins to become independent of the central nervous system as far as cellular contribution is concerned, the rami communicantes becoming purely fibrillar. On the thirteenth day the network aspect of the sympathetic system disappears in the anterior region of the embryo, where a true cellular cord is formed without segmental thickenings. The amount of sympathetic tissue increases more and more, especially at some levels such as the adrenals and the gonads. Kohn doubts, however, whether all those sympathetic elements are directly derived from the prevertebral chains, because for the gonads at least the sympathetic chain has probably not yet grown so far back. On the fourteenth and fifteenth days three regions can be distinguished in the sympathetic cord. In the cervical region it is purely a cellular, well defined band extending to the level of the pharynx. The medial or trunk region shows a fibro-cellular chain, while in the caudal region, caudally to the pronephros, it keeps the

reticular aspect of the primary anlagen. In sixteen day embryos appear the sympathetic ganglia with the fibrillar connecting commissures. The differentiation of the sympathetic cells in the chain begins only at the seventeenth day to be complete around the twenty-first, while the elements of the peripheral ganglia are already differentiated in typical ganglion cells around the seventeenth day.

Poll in 1904, studying a complete series of *Emys europaea*, described very completely the origin of the cortical part of the adrenal from the peritoneal epithelium and of the chromaffin part from the anlagen of the prevertebral plexuses. In a later paper he dealt with the organogenesis and the histogenesis of the chromaffin tissue and traced the evolution of the primitive sympathogony into either sympathoblast and later sympathetic ganglion cell or phaeochromoblast and phaeochromocyte.

Whitehead ('03) in a 13 mm. long pig embryo described sympathetic ganglia located dorsolaterally to the aorta, nearly opposite the dorsal border of the Wolffian body and connected with the spinal nerves by splanchnopleural branches; numerous smaller collections of sympathetic ganglion cells with many mitotic figures could be seen scattered on each side of the aorta. At 16 mm. chains of ganglia of various sizes appear between the aorta and the cortical anlagen of the adrenals; from these ganglia nerve fibers grow out and accompanied by numerous cells run lateralwards along the ventral and the dorsal aspects of the adrenals. At 30 mm., the capsule of the adrenal primordium breaks up, and a direct connection is achieved between the sympathetic ganglion cells and the cortical part of the adrenal. The cortex develops a long time before the migration of sympathetic elements; it is first seen in 8 mm. embryos and is derived from the peritoneal epithelium.

In 1907 Froriep, studying embryos of *Torpedo* and of the rabbit, described medullary cells migrating along the ventral roots of the spinal nerves. In a first paper he considered those cells as giving rise to the neurilemma, but after the conclusive experimental results of Harrison ('04) showing that the sheath cells of both ventral and dorsal roots take their origin in the neural crest cells, he concluded that the migrating cells found along the motor roots and from the spinal ganglia along the dorsal roots give rise to the sympathetic nervous system. He asserted that all the sympathetic neurones in the prevertebral chains and plexuses arise from the ventral half of the nervous system and he looked toward the realization of experiments proving that the removal of the neural crest does not interfere with a normal development of a complete sympathetic system.

London and Pesker ('06) studied the development of the peripheral nervous system in mammalian embryos. Their researches deal with the histogenesis of the nerve endings in striated and in smooth muscles, in heart muscle and in cutaneous epithelium. Their paper represents the first attempt to study the embryology of the nervous endings, but it is too incomplete to draw definite conclusions. The nerve endings in the smooth muscle develop in the same way as those in the striated musculature, although there is some shortening of the developmental stages. The heart ganglion cells are considered as true sympathetic cells, as had already been shown by Aronson, His, Jr., Arnstein and Smirnow.

In a series of papers Streeter ('08, '12) described the peripheral nervous system of human embryos; though no very extensive account of the sympathetic nervous system is to be found, many interesting details are described dealing with the

neural crest in the occipital region and the distribution of the cranial nerves. In a 10 mm. embryo the peripheral migration of sympathetic elements is completed, forming on each side of the body a longitudinal column, lateral to the aorta, extending from the occipital region to the lower sacral vertebrae; from the sixth to the tenth thoracic segments a definite fibrocellular plexus forming the splanchnic nerves and the coeliac plexus is found.

Carpenter and Main ('07) studied the migration of medullary cells into the ventral nerve roots of pig embryos. In embryos 11 mm. in length, breaches of considerable extent appear in the external limiting membrane of the spinal cord; through these, medullary cells are passing into the nerve roots. Such cells can be seen just inside the external limiting membrane, in an intermediate position half in and half out of the neural tube and in the basal part of the nerve root just outside the tube. Harrison saw also medullary cells migrating into the ventral nerve roots of salmon embryos and had already suggested the possibility that these cells may follow the visceral branches of the spinal nerves into sympathetic ganglia and there give rise to motor neurones. Carpenter and Main emphasize the difficulty of a definite answer to the question whether or not any of those migrating cells corresponding to the indifferent cells of Shaper, become the nerve cells of the sympathetic ganglia; they note with interest that Kölliker described true ganglion cells in the ventral nerve roots of adult cats.

Cajal ('90, '92, '95) reserved his opinion as to whether the sympathetic neuroblasts migrate along the ventral or the dorsal roots of the spinal nerves. Using the silver impregnation method on chick embryos, he tended to the view that they wander out along the ventral roots before

the moment the anterior roots become fibrillar and when the cells are still apolar.

Held ('09) published a very important piece of work dealing with the peripheral nervous system in the entire series of vertebrates. He tried to show that in all vertebrates the cells found along the motor roots do not play any rôle in the development of the sympathetic system, which is entirely derived from the spinal ganglia. In a 12 mm. embryo of *Acanthias*, the dorsal root is extraordinarily rich in migrating elements, while the motor root is practically fibrillar; the fusion of both roots to form the mixed spinal nerve is found more ventrally than it usually is, at a point where the dorsal root has already given off its sympathetic thickening. In all the selachians, the sympathetic cellular aggregates appear at the median side of the spinal nerves. Inasmuch as the fibers of the sensory and of the motor roots of the spinal nerve do not mingle with each other but grow peripherally as distinct fiber bundles, of which the sensory lies mesial to the motor, the cellular elements of the sympathetic anlagen are in immediate contact with the sensory fibers and have no apparent relation to the motor fibers. Anatomically and embryologically the sympathetic anlagen are exclusively connected with the dorsal roots and with the spinal ganglia. In amphibians the earliest trace of cellular migration from the spinal ganglia is observed at 5.75 mm. In this group, cells migrating along the ventral roots never occur, and here at least the sympathetic anlagen have necessarily their origin in the spinal ganglia. Furthermore, the physiological experiments of Steinach ('94) on *Rana esculenta* have proved that the posterior spinal roots contain visceral motor fibers to the stomach and the intestinal tract. In the other groups, Held admits the real existence of a cellular mi-

gration along the ventral roots. The migration, very abundant in the reptiles, is very poor in other vertebrates, but he does not eliminate definitely a possible rôle of those cells in the formation of the sympathetic anlagen and he leaves the question unanswered.

Marcus ('09) stated that the cells described by Froriep along the ventral roots do not migrate from the spinal cord but from the neural crest. In early stages of *Torpedo* he was able to observe cellular chains connecting the neural crest with cell aggregates situated in the ventral roots, those connections being found before the first differentiation of the spinal ganglia. He, therefore, admits that the neural crest represents the only primary source of the sympathetic neurones.

Hoven ('10) studied extensively the histogenesis of the peripheral nervous system in chick embryos. Though the most important part of his work deals with the cytological processes of differentiation of the neurofibrils, he gives interesting data concerning the organogenesis of the nervous system. Using the silver nitrate impregnation methods, he shows that the very first appearance of the ventral roots as growing neurites of intramedullary neuroblasts takes place at 76 hours of incubation. He never found any migration of cells along the motor root and considers that the cells described by Balfour ('78), Marshall ('78), Dohrn ('91), Pighini ('04), Froriep ('07), Held ('09), Carpenter and Main are purely mesenchymal cells. The sympathetic ganglia are derived from the spinal ganglia and are very clearly observed at 79 hours of incubation. For him the sheath cells are of mesodermal origin.

In numerous papers Ganfani ('08, '12, '14, '16) described the sympathetic trunks arising from neurocytes which advance peripherally along both the dorsal and ventral roots of the spinal nerves. The

enteric plexuses are developed from the anlagen of the sympathetic trunks, from which cells migrate further ventrally than those contributing to the formation of the prevertebral plexuses. We shall refer to this investigation later on. In a short paper, Meikelljohn ('08) studied the development of the visceral nervous system of the digestive tract in the chick, by the silver impregnation method. At five days, vagus fibers are described entering the stomach, forming in its wall a primordium of Auerbach's plexus. The plexus is formed by fine fibers given off by mono- or bipolar cells. In the lowest part of the intestine, a few bipolar cells and a few fibers seem to rise from the cord in the position of the nervi erigentes. At six days the vagal contribution to the stomach is more abundant and there has developed a rich network of delicate fibers, apparently representing the sympathetic supply. In the lower part of the intestine, a chain-like arrangement of cells and numerous fibers is found innervating its cloacal end. The other parts of the intestine show a few scattered cells and fibers without clear plexiform arrangement. This preliminary note, illustrated by very schematic drawings, shows the important part played by the sympathetic system in the innervation of the alimentary canal; the oesophageal plexus and the gastric Auerbach's plexus are the only structures derived from the vagus and are soon invaded by the sympathetic supply.

W. Lewis and M. Lewis ('12) studied a culture of sympathetic nerves from the intestine of chick embryos in saline solutions; the growth of the nerve fibers occurs in ten per cent of the cultures and is observed with equal frequency in taking intestinal fragments of chick embryos from eight to thirteen days of incubation.

In the *Human Embryology* of Keibel and Mall, Streeter (1914) made a very impor-

tant contribution concerning the development of the sympathetic nervous system in man. At 4.5 mm. of length cells from the loose ventral border of the spinal ganglion detach themselves and extend ventralward in advance of the ventral roots. The migration of sympathetic cells is accomplished by a pure wandering through mesoderm rather than along preestablished nerve fiber paths. By the time a well defined nerve trunk is differentiated, the sympathetic cells have already completed that part of their migration and the cells still found along the nerve trunks are only sheath cells. In a 7 mm. embryo the migration of cells into the sympathetic anlagen is in active process and cellular rami communicantes are present in some regions. At 9 mm. in length the ganglionic prevertebral cords and the splanchnic nerve plexuses are definitely outlined. At 6 mm. the visceral ganglia and the sympathetic ganglia situated in the head region are to be seen with their connecting branches. Carpenter ('06) had already shown that in the chick the ciliary ganglion consists of two portions, a small dorsal sympathetic part derived from the semilunar ganglion and a larger ventral part containing large bipolar cells derived from the neural tube by migration along the oculomotor nerve. Froriep ('07) described, in *Torpedo*, cells wandering out from the central nervous system together with the growing oculomotor fibers and fusing with the cells derived from the trigeminal ganglion so as to form a composite ganglionic mass. Streeter does not see any migrating cells along the oculomotor nerve in the human embryo. The ciliary ganglion consequently consists here exclusively of wandering cells from the semilunar ganglion. He assumes that as well as for the sympathetic anlagen of the trunk, their migration occurs very early, probably just in advance of the developing nerve fibers

and that it is not until they have reached their permanent position that they undergo an active proliferation and form a compact cellular mass. The sphenopalatine and submaxillary ganglia are probably derived entirely from the semilunar ganglion, though through their connections with the geniculate ganglion of the facial there is a possibility of a facial contribution. In the same way the otic ganglion is developed in intimate relation with the semilunar ganglion containing perhaps a few cells coming from the glossopharyngeal nerve through its tympanic branch.

R. Camus ('13) studied in considerable detail the development of the sympathetic nervous system in frog embryos. The first trace of sympathetic Anlagen appears as isolated cells slightly different in cytological characters from the mesenchymal cells, presenting prolongations in direct continuity with those of the latter cells. In the spinal nerves no cellular elements are found besides the Schwann cells. For these two reasons he believes in the mesodermic origin of the sympathetic Anlagen. At a later stage, the sympathetic ganglia are formed by a syncytium, the peripheral part of which is still in direct continuity with the mesodermal strands. About the same time appear the communicating rami, which the author identifies without any hesitation with the fibers of the mesenchymal net. At this moment the cells of the communicating rami, the true mesenchymal cells and the future ganglion cells are all in direct protoplasmic continuity. He admits further that the sheath cells arise from mesenchymal cells, the plasma of which differentiates in neural fibers. He describes neuroblasts in the intestinal wall at 6 mm. in length, giving rise to numerous independent small ganglia which become connected with the spinal nerves at the stage of 14 mm. Although this piece of work is a very voluminous one, one can

not help being very sceptical about most of the observations. His isolated nerve cells either in the prevertebral region or in the intestinal wall are most probably ordinary connective tissue cells. The syncytial origin of the nerve fibers, the mesodermal origin of the sheath cells, the local differentiation of the communicating rami are only easy answers to questions unsolved by incomplete observations.

Miss Abel ('09-'12) published two successive papers on the development of the sympathetic nervous system in chick embryos; only the second one, a correction of the first one in the light of new observations, is to be taken into account. In a 60 hour embryo the silver impregnation shows in the mesoderm, close to the spinal cord, a few cellular elements larger and darker than mesodermal cells. At 72 hours occurs a very abundant migration of cells from the spinal cord into the spinal ganglia and from the ventral margin of the spinal ganglion into the beginning posterior root. At 80 hours of incubation there is a considerable increase of the cellular migration from the spinal ganglia forming a delicate chain running in the neighborhood of the aorta. A poor migration is also found along the anterior roots. These migrating cells are either indifferent cells of Schaper or true neuroblasts. At 108 hours the sympathetic chain is well developed on either side of the notochord behind the aorta, within the abdominal region a well marked ventral migration to the ventral aspect of the aorta. Somewhat later appear fibrillar communicating rami. In embryos of 144 hours the formation of the ganglia of the secondary or permanent sympathetic chain is first seen in the thoracic region. They are largely formed by the grouping of sympathetic cells which accumulate between the spinal nerves and the temporary sympathetic chain. The portion of the

latter which is not incorporated in the permanent chain gradually disappears. In the abdominal region the ventral migration of sympathetic cells to the abdominal and visceral plexuses was already so extensive that it is impossible to distinguish the temporary and permanent sympathetic chains. A special sympathetic supply is found along the vagus nerve, coming from the hind brain to the ganglia of the glossopharyngeal and vagus nerves. The cells found in this part of the sympathetic are characterized by the smaller cellular size and a less pronounced reaction to silver nitrate. From the vagal sympathetic supply, cells are found in the heart at 108 hours, in the stomach at the same moment, in the oesophagus, liver and pancreas at 144 hours. From the sympathetic pre-vertebral chains cellular outgrowths are penetrating into the walls of the gut around the stage of 144 hours, although in the large intestine the ganglion of Remak is already present at 108 hours and runs along that part of the digestive tract for a certain distance.

Roud ('03) believed in the mesodermal origin of the sympathetic nervous system, and Bruni ('16) extended in this sense his observations on *Gongylus*, chick and rat embryos. He described two successive anlagen. The first in a chronological order is mesenchymal, the second having an ectodermal origin. The mesodermic primordium is for the first time to be found dorsolaterally to the aorta at a position corresponding to the cephalic part of the mesonephros, and from this point it extends in both cranial and caudal directions. When this mesodermal sympathetic chain is formed, true neurocytes originating from the neural tube migrate towards the aorta and by the way of communicating rami the ectodermal generation of sympathetic cells becomes connected with the mesenchymal anlage. Following Bruni

the mesenchyme-derived cells would act as chemotactic mechanism attracting the ectodermal cells, and he finds a basis for this idea in the existence of cytoplasmic granulations in the cells of the mesenchymal anlage. This anlage loses progressively its importance, its place being taken by the ectodermal neurocytes, except in a few places such as the abdominal plexuses where it develops, proliferating all around the aorta and showing the cytological differentiation into chromaffin elements. The chromaffin tissue would thus have a purely mesenchymal origin.

In 1915 and 1917 C. Da Costa studied very carefully the histogenesis of the adrenals and of the chromaffin tissue in the cat and in a few species of Cheiroptera, describing at the same time the development of the sympathetic nervous system. He found the first trace of this system in a 5 mm. embryo of *Myotis* or of *Vesperugo*. These anlagen were formed by a few cellular elements located at the dorsolateral angles of the aorta and were differentiated very easily in the surrounding mesenchyme by a slightly greater stain avidity. There were yet no communicating rami, though in an embryo of *Miniopterus* of 4.5 mm. the sympathetic anlage was near enough to the spinal nerves to suggest its origin from these nerves. The first sympathetic cord is thus found without any connection with the central nervous system, and this author supports the description of Paterson, Fusari and Bruni, suggesting, however, the possibility of an earlier migration. The connection with the central nervous system by the way of the communicating rami appears first in the thoracic and abdominal regions. The cervical part remains free a much longer time from those connections, though its moniliform aspect reveals its segmentary origin. He shows very clearly the derivation of the chromaffin cells from the sympathetic ele-

ments and suggests the name of protosympathetic cells to designate the sympathetic elements before their differentiation either into true ganglionic cells, chromaffin cells or sheath cells. In the 5 mm. embryo of *Myotis* the sympathetic system is represented by cellular strands, composed of only one cellular type with deeply stained cytoplasm and a round richly chromatic nucleus. In a 7 mm. embryo two cellular types can be easily distinguished in the sympathetic anlagen. One of them shows the characters described at the preceding stage, while the other one shows an elliptical nucleus with poorly represented chromatin. The second type characterizes the chromaffin cells. Although no clear transitions could be found between the two cellular types, these careful observations support the theory of the sympathetic origin of the chromaffin cells. As far as the primary origin of the sympathetic system is concerned, the author leaves the question unanswered, requiring further study.

W. Allen ('19) shows that in the embryonic life the motor and sensory fibers of all the spinal nerves of *Polistotrema* and *Squalus* pass to the periphery as separate motor and sensory rami, each ramus possessing a ventral and a dorsal root. He agrees with Onodi ('86) that the prevertebral sympathetic ganglion cells of *Squalus* are derived entirely from neural crest cells which have migrated along the ventral root of the sensory ramus at a time when both roots of this ramus are completely separated from the corresponding motor rami. The few cells which pass out of the neural tube with the ventral root fibers are apparently only concerned with the formation of neurilemma.

Steward ('20) published a beautiful piece of work concerning the cranial sympathetic ganglia in the rat. In an embryo thirteen days old the existence of the

superior cervical ganglion and of the carotid nerve is not yet constantly found. Twelve hours later the cervical sympathetic ganglia show a clear tendency to fusion and to a forward extension along the internal carotid artery to a region just dorsal to the pharynx at the level of the second pharyngeal pouch. At fourteen days unipolar neuroblasts migrate out of the superior cervical sympathetic ganglion and insinuate between the fibers of the carotid nerve to join the great superficial petrosal. The vidian nerve may be followed into the sphenopalatin ganglion and with it apparently run an important number of fibers from the superior cervical ganglion. In a sixteen days old embryo the carotid nerve can be traced as far as the carotid canal, with ganglion cells scattered throughout its length. At seventeen days the internal carotid nerve after giving a branch to the hypophysis fuses intimately with the abducens; the latter, soon after this fusion, gives a small anastomotic branch to the trigeminal nerve and numerous ganglion cells are found along it. As far as concerns the vagus portion of the sympathetic, Steward is unable to trace the ultimate origin of the migrating indifferent cells found along it. He emphasizes the real difficulty of determining whether they arise from the neural crest or from the neural tube. He describes numerous neuroblasts along the vagus nerve but never found a direct continuity between them and the vagus ganglia. Migrating cells were found as far as the cardiac plexus. At fifteen days and six hours, numerous neuroblasts are found in the gastric and intestinal plexuses. As regards their origin the addition of elements from the trunk sympathetic system must be excluded, since there is no indication of connections between the coeliac sympathetic and the vagus fibers. The former at this stage do

not yet enter the gastric or intestinal territory. In the vagus trunks two types of neuroblasts are to be found. The first cellular type, of large bipolar cells, is mostly found in the cervical region and becomes very rare below the origin of the recurrent nerve; the second type, of much smaller cells, identical to the true sympathetic neuroblasts, is particularly represented in the pulmonary, cardiac, gastric and intestinal branches.

In 1918 Erik Müller and Goran Liljestränd studied physiologically the autonomic nervous system of rays and sharks. One of the outstanding results they obtained was that the main motor pathway to the intestinal tract was through the ventral roots of the trunk spinal nerves. Since the sympathetic ganglia seem to arise from the spinal ganglia of the dorsal roots, they thought necessary to carry out new anatomical and embryological studies on that point.

In *Squalus acanthias* Müller ('20) finds the first primordia of the sympathetic system in 14 to 17 mm. embryos. Both ventral and dorsal roots present a central fibrillar aspect surrounded by numerous cellular elements which are perhaps more numerous even along the ventral root than along the dorsal one. Those cells, without any doubt, originate from the spinal cord, from the ventral root elements and from the spinal ganglion of the dorsal. At 17 mm. a very clear differentiation is to be observed, the migrating cells along the ventral roots become flat and can not be stained by Bielchowsky's method, while those originating from the spinal ganglia keep their round aspect and are more and more intensely stained with the same technique. At this stage the roots do not show any connection with each other. Immediately after the end of the dorsal root swells into a small ganglionic mass representing the first anlagen of the sympa-

thetic nervous system, of which the origin is doubtless exclusively in the cells migrating from the spinal ganglia along the sensory roots. Still no fusion can be found between the two roots. In 24 mm. embryos the sympathetic ganglia are still in very intimate connection with the dorsal roots. Although both roots are still entirely distinct from one another, fibers from both of them are penetrating into the sympathetic ganglion where they terminate in typical club-shaped endings. Though exclusively derived from the dorsal root ganglia, the sympathetic ganglia receive fibers from both roots. The further development does not offer any particularly interesting point, although Hoffman's statements, that no sympathetic chains are found in selachians and that the sympathetic ganglia corresponding to the ten first spinal nerves degenerate, are proved to be erroneous.

In his description of the vagus ganglion of the selachians, Landacre ('16) was unable to find any structural differentiation between the cellular territories of the ganglion. Müller ('20) distinguishes very striking differences between them. In 26 mm. embryos, the dorsal part of the ganglion contains big, round, regularly bipolar elements and gives origin to the ramus lateralis vagi. The motor medullary nucleus is well defined and from it arises a group of fibers going to the medial part of the ganglion. This latter is formed by smaller cells, among which some show a very rich neurofibrillar distribution, while others are stainless and show small prolongations or are apolar. Small fibrocellular branches grow out of the ganglion, penetrating soon after into the walls of the digestive tract where they present the aspect of a network. At 35 mm. the entire stomach is surrounded by the vagal plexus. The cellular elements found along these branches show the structural characters

of the cells of the vagus nucleus. Their migration from the ganglion is particularly marked in 30 mm. embryos, while in 32 mm. embryos the big trunks near their origin become fibrillar, the cells migrating more peripherally in the small branches. In 35 to 38 mm. embryos along the vagus fibers are found, besides the round isolated neuroblasts, cellular elements containing two or more nuclei, in which the nervous substance is so deeply stained and fills the cell body so entirely that no fibrils can be detailed in their cytoplasm. Most of this vagal network is located inside the external muscular layer, though nerve cells and fibers are found all over the musculature as well as in the mucous membrane. Some have their endings just beneath the epithelium and look like real sensory cells. From the gastric territory numerous fibers pass directly into the walls of the small intestine.

In a later work, Müller ('21) describes in the digestive tract of the selachians two types of nerve cells connected by numerous anastomoses and forming a real network. The first type, existing between the two muscular layers, in the muscularis mucosae and in the mucous layer, is characterized by round, oval or polyhedral cells with a well developed internal neurofibrillar structure. The second cellular type, almost localized in the mucous layer, consists of flattened, ramified cells, generally isolated and possessing poorly developed neurofibrils. The study of their embryonic development shows that the first cellular type originates from vagus ganglion cells migrating along the growing vagus trunk toward the stomach and the intestine; the second type is derived from the trunk sympathetic system. In a five day chick embryo the vagus nerves can be followed to the stomach, the rest of the digestive tract presenting as the only nervous structure the nerve of Remak originating from

the pelvic sympathetic. Somewhat later the vagus territory extends to just below the hepatic duct. There is at that stage no migration of cells and no outgrowth of fibers from Remak's nerve. The upper part of the small intestine below the hepatic canal is entirely lacking in nerve elements. In the vagus territory the neuroblasts are grouped in small collections. They possess a clear neurofibrillar structure and show the cytological characters of the cellular type already described in selachians. The region belonging to the nerve of Remak does not show a migration of neuroblasts and nerve fibers in the intestinal wall until the seventh day of incubation and the migrating cells correspond to type II. On the eighth day of incubation it becomes possible to distinguish the Auerbach and Meisner plexuses in the aspect of distinct networks from which branches can be followed to Remak's nerve. These sympathetic networks are entirely different from those characterizing the vagus territory. The fibers are rare, the cells closely disposed near one another, while in the vagus plexuses the neuroblasts are isolated by a rich fibrillar structure.

In 1893 Cajal described in the intestinal wall of frogs and of various mammals asteroïd cells with four or more long prolongations which seldom divide. While in those cells Dogiel distinguishes numerous dendrites and one neurite, Cajal and Müller admit that all the prolongations are of the same type. Besides those asteroïd cells Cajal noticed the presence of fusiform or triangular small cells with many branches dividing frequently at right angles: they are free neurones existing with real frequency in all layers of the intestinal wall.

Müller ('94) using the Golgi method finds in the intestinal wall and in the pancreas small ramified cells with numerous

identical prolongations. Dogiel one year later shows beautiful pictures of these interstitial cells, of which the branches seem to form real nets identical with those found in invertebrates. Dogiel and Kölliker believe those elements to be specialized connective tissue cells. La Villa with the methylene blue technique admits their real nervous nature on account of their avidity for the methylene blue, their general morphological characters and the various aspects of their prolongations. Cajal confirms this interpretation and shows that after silver impregnation the neurofibrils of the interstitial cells appear even better developed than in the cells of the Auerbach plexus. Müller too admits the nervous nature of the interstitial cells but corroborates the description of Dogiel in so far as the existence of anastomoses going directly from one cell to another is concerned. Heidenhain and Huber consider the interstitial cells as connective tissue elements. Dogiel ('95-'96) believes that the intestinal nervous system as well as the cerebrospinal nervous system is able to show reflex arcs which take place between the sensory cells of type II and the type I exciting the muscular layers. This is not necessarily true, for first of all, many authors do not see any difference between the numerous prolongations of these cells. Furthermore, no synaptic connections have ever been described.

In the higher vertebrates we have no longer the diffuse intestinal nervous system found in selachians but besides the connecting neurones we have interstitial cells. The result of such a disposition is that the conduction of stimuli is no longer reversible but is always similar to the axone reflex of Langley. The two cellular types found in the intestine must have, as in the rest of the autonomic nervous system, antagonistic functions. The vagus cells must be motor, the sympathetic

cells inhibitory. It is, furthermore, well known that in the intestine any excitation produces a contraction at that level with a concurrent inhibition of the musculature just below. The vagus motor elements must be disposed so as to conduct the stimulation a short way, whereas the sympathetic neurones with their long prolongations and their arrangement in long series of cells are able to convey the inhibition farther away. In the stomach on the contrary such inhibitions do not take place. We observe a contraction wave, called *catastalsis* by Cannon, followed by an inverse contraction, the *anastalsis*. This physiological observation is in complete agreement with the fact that we have here an almost pure vagal plexus. The small inhibitions observed by Cannon after stimulation of the stomach might correspond to the few sympathetic cells in the muscularis and in the mucous layer.

Froriep ('07) was the only man who tried to apply the physiological conceptions of Langley and of Gaskell to the facts shown by embryological observation. He felt that the nerve fibers of the efferent visceral components grew along the ventral roots; the cell bodies remaining in the spinal cord or following the growing fibers to give rise to sympathetic ganglia. The observations of Müller modified this scheme in showing that the prevertebral sympathetic ganglia arise exclusively from the spinal ganglia and that the preganglionic fibers of the efferent visceral elements grow only secondarily in them; the cell body remaining in the spinal cord.

The enteric system shows a more complicated organization and Langley considered it as a special part of the autonomic system, with a particular cellular morphology, a very intricate connection with the central nervous system and an atypical way of reacting to the testing drugs. Gaskell, to answer that question, admitted

that in the Auerbach and Meissner plexuses the vagus fibers originating from cells lying in the central nervous system show their endings. Those preganglionic fibers are in connection with vagal ganglionic cells from which the postganglionic fibers pass to the musculature. On the other hand the sympathetic inhibitory fibers come directly from the prevertebral sympathetic ganglia to the musculature without having a local relay. This scheme does not consider the existence of any sympathetic cells in the intestinal wall and this fact is now definitely shown. Müller admits that the intestinal nervous system differs from the general autonomic system in presenting a third relay by way of the migrating cells into intestinal walls. The sympathetic and vagal systems are in this way identical. The vagus ganglion corresponds to a vertebral spinal ganglion, the visceral part of which has remained within the nucleus of origin, while the visceral part of a spinal ganglion isolates itself in forming the prevertebral sympathetic ganglion. The intestinal neuroblasts are the third relay both for the vagal and the sympathetic systems.

Müller and Ingvar ('21) studied very carefully the development of the sympathetic system in amphibians. They confirm the description given by previous authors, especially by Held ('09), concerning the ectodermic origin of the sympathetic nervous system, its cellular elements being migrating cells from the spinal ganglia. They were able to carry out the famous experiments of removing the dorsal half of the spinal cord in young embryonic stages, obtaining in that way a total absence of sympathetic anlagen. Their embryos did not live more than fourteen days, some of them entirely lacking a trunk sympathetic system.

The same authors using Bielchowsky's technique were unable to find any isolated

sympathetic cells in the prevertebral mesenchyme of chick embryos. They believe that the cellular elements described by Cajal at 52 hours and by Held at 60 hours might be connective tissue cells possessing an argentophile intracellular reticulum. In destroying the ganglion crest of young embryos by means of electrocauterization, they produce the absence of sympathetic anlagen in the injured segments. The ganglion crest seems to be the only source of sympathetic elements. The two series of normal morphological observations are strikingly confirmed by the experimental results and they constitute strong evidence in favor of the theory that the origin of the sympathetic primordia is from the neural crest by migration of its elements along the dorsal roots. Kuntz and Batson ('20) also made an experimental study on the same groups, but obtained exactly inverse results. We shall not discuss this work of Kuntz at present since we are going to consider his very important contribution as a whole.

In a very extensive and careful piece of work, S. Rau and P. Johnson ('23) studied the development of the sympathetic nervous system and of the suprarenal bodies in the sparrow. Taking into special account each one of the three possible origins of sympathetic elements, the neural crest, the dorsal root ganglion and the ventral root, they hold that the sympathetic primordia are derived from three sources and their drawings try to illustrate this. The neural crest contribution is to be seen in embryos of five to seven somites, corresponding to a 32-hour chick embryo. The crest at this moment reaches the ventral edge of the spinal cord and numerous cells are wandering into the mesenchyme between the neural tube and the aorta. These isolated cells show the cytological characters of the crest and are very clearly distinguishable from the mesenchymal

cells. In a somewhat older embryo corresponding to a 42 hour chick, true neuroblasts can be seen migrating from the spinal root ganglion toward the dorsolateral angles of the aorta. Still later some cellular migration can be seen from the ventral half of the spinal cord along the ventral roots to the same aspect of the aorta. While it appears that many of these migrating cells are sympathetic in nature, the possibility must not be excluded that some of them will develop into the sheath cells. In the early stages, the sympathetic primordia are arranged metamerically and almost located in the intersomitic regions. Later stages show the growth of longitudinal cellular strands uniting the dispersed cell masses into two parallel continuous moniliform chains, of which the authors modeled very careful reconstructions. In later stages the primary ganglionic swellings of these cords send dorsolateral extensions, the free ends of which enlarge and, becoming separated from the primary ganglia, give rise to the definitive sympathetic ganglia and to the secondary sympathetic chain. As far as concerns the communicating rami there has arisen a considerable amount of confusion owing to the fact that there exist three sets of connections between the sympathetic primordia and the central nervous system: the cellular strands giving rise to the primary cords, the dorsal extensions of those to form the secondary chains and the permanent connections between the secondary sympathetic ganglia and the nerves. Ganfani ('16) goes so far as to use the terms primary, secondary, and tertiary rami. The two first communicating branches have only a transient existence except for a possible rôle in the constitution of some visceral plexuses. The contributions of the sympathetic system to the suprarenals all arise from the primary sympathetic cords at the very moment

when they are sending their dorsal extensions to give rise to the secondary chains.

The triple derivation suggested by Rau and Johnson represents the most conciliatory idea that will bring agreement among the different investigators. One can not help doubting the soundness of this attempt. The neural crest contribution does not seem to be a very important one. The migrating cells along the ventral roots might just as well represent sheath cells. The dorsal root ganglion origin is the only definite one and anyhow is by far the most richly represented. Their idea about a possible rôle of the primary chains in the formation of visceral plexuses has found a very striking confirmation in a recent work of Willier ('28).

Goormaghtigh ('14-'21) studied the development of the coeliac plexus and of the adrenals in the chick embryo. He considered the sympathetic chains as originating from true ectoblastic ganglionic cells, while the chromaffin elements were mesodermic in origin. In 1924 he modified entirely his conception. In a 50 hour chick embryo, cellular bands are migrating from the dorsal part of the nervous system toward the dorsolateral angles of the aorta. They represent the neural crest. This neural crest differentiates into three segments: the dorsal one gives rise to the spinal ganglia, the middle one is the source of the Schwann cells, and the ventral one contributes to the formation of the primary sympathetic chains. The secondary or permanent sympathetic cords are formed by migration of medullary elements along the ventral roots at the stage of 73 to 78 hours of incubation. At the same time the primary chain regresses, its elements acquire a glandular structure, numerous blood vessels penetrate into the cellular mass. These transformations represent the differentiation of the chromaffin tissue. The chromaffin elements are derived

from the neural crest, while the sympathetic ganglion cells are wandering out of the neural tube along the ventral roots. It is possible that the sheath cells of the visceral nerves are derived from the elements of the regressing primary chains.

F. Tello ('25) studied the histogenesis of the sympathetic nervous system in chick embryos using the silver impregnation method. The first traces of the primary sympathetic chain appear in the second half of the third day. At the posterior aspect of the aorta he describes a few isolated cells showing a delicate neurofibrillar differentiation. They are entirely independent of the spinal mixed nerves, which pass along the internal border of the myotome. The silver impregnation and the neurofibrillar structures are very clearly marked and there can be no doubt about the nervous nature of those elements. Progressively the sympathetic primordia concentrate around the point of origin of the intersegmental vessels and the prevertebral primary sympathetic cords are formed. At the beginning of the fifth day the sympathetic neuroblasts of this continuous chain show a dorsipetal migration toward the point of junction of the anterior and posterior spinal roots. The most dorsally situated elements show numerous mitotic figures, giving rise to cells which migrate forward or backward in order to connect with the elements of the preceding or following segment. Around the sixth day the secondary sympathetic chains are constituted. They are located very near the fusion of both spinal roots and they soon acquire definite connections with them through communicating rami. Thus Tello admits the exclusively mesodermal origin of the primary sympathetic primordia. They immediately concentrate into a continuous bilateral chain. The permanent sympathetic chains are entirely derived from the migrating elements of the pri-

mary ones and are not originated from the central nervous system.

Taking into special account the structure and development of the gastrointestinal plexuses, Tello describes in the three-days old chick embryo isolated fusiform elements at the level of origin of the hepatic and pancreatic diverticula. These cells send off numerous anastomitic branches, giving rise to a well defined gastroduodenal plexus extending upon the stomach and the anterior part of the small intestine and which in the following days mingles its fibers with the terminal fibers of the vagus nerve. The posterior intestine, from the end of the duodenum to the cloaca, is innervated by the ganglionated nerve of Remak originating from the aortic plexus and penetrating into the intestinal wall by its juxtacloacal extremity. In 4 mm. long mice embryos, the stomach and the anterior part of the intestine show a very rich layer of nervous elements between the entoderm and the splanchnopleural sheet. At that time the vagus nerve ends in the very upper part of the stomach, the splanchnic nerves are not yet formed and the visceral branches of the spinal nerves do not reach the ventral aspect of the aorta. The neuroblasts just described have necessarily a local, mesodermal origin. In 10 mm. embryos the submucous plexus, exclusively fibrillar, sends numerous fibers ramifying between those cells. The posterior part of the intestine remains without any innervation until the stage of 12 or 13 mm. when its nervous supply arises by a very small extension from the anterior intestine and from the superior and inferior mesenteric plexuses. In the anterior intestine the Auerbach plexus is alone present in the stage of 15 mm. At this time the mesenteric plexuses have appeared and in the intestinal wall the smooth muscle layer and the plexus of Meissner make their appearance. Weber

('51) described a human foetus of about full term in which brain and spinal cord were entirely absent, although the peripheral nerves and the sympathetic nervous system were normally developed. Dart and Shellshear ('21) have interpreted this and other similar cases in which peripheral nervous elements are found in the absence of the cerebrospinal nervous system as being a demonstration of the mesodermal origin of the peripheral nervous system including the sympathetic system. Lehman ('27) also considers those cases as supporting his theory of the mesodermal origin of the spinal ganglia. It is most probable that such an interpretation does not correspond to the facts and that in these cases the central nervous system must have undergone degeneration after the peripheral system had arisen. Furthermore, a few contradictory cases were reported, especially by Alessandrini (1829), who describes a calf born with an absence of spinal cord in a few thoracic segments and in which the spinal nerves and sympathetic trunks were absent in the corresponding region. Those cases afford no evidence of value regarding the origin of the sympathetic system, since the previous history is entirely unknown.

In various publications Ganfini ('08, '12, '14, '16) studied the development of the sympathetic nervous system in numerous groups of vertebrates. His careful observations represent a new attempt to admit a mixed origin of the sympathetic Anlagen instead of an exclusive derivation from one or another part of the central nervous system. In *Amia calva* he finds the primordia of the sympathetic system in 6 mm. embryos. The spinal nerves are already completely formed and numerous neurocytes are found along the ventral as well as along the dorsal root. In 12 mm. embryos true sympathetic ganglia are well isolated in the surrounding mesenchyme.

Soon after, they connect with one another, forming a continuous bilateral chain. The two chains unite at the level of the eighteenth spinal nerve, forming there the pre-aortic sympathetic commissure. In 15 mm. embryos the sympathetic chains extend cranialwards to the acousticofacial ganglion; the cellular differentiation is nearly complete and true ganglionic cells are found. At 20 mm. he distinguishes four regions. In the cranial region the sympathetic shows a plexiform aspect surrounding the aortic and carotid vessels, being close to the vagus nerve and the first spinal nerve without showing any connections with them. In the first five spinal segments the sympathetic ganglia are disposed in regular correspondence with the communicating rami, numerous small efferent branches growing toward the aorta. From the sixth to the thirtieth spinal nerve there exists a rich plexiform sympathetic system with frequent fibrillar anastomoses. In the fourth region the ganglia are regularly arranged. The intestinal nervous system is a direct outgrowth of the sympathetic chains. The motor root when alone, is still able to differentiate a sympathetic ganglion. In two occipital nerves he found the absence of spinal ganglia and of dorsal roots and in spite of that the existence of clusters of neurocytes at the angle of the carotid.

In 5.5 mm. embryos of *Chrysemys marginata* the first twelve spinal nerves are present and both roots are formed by big round cells showing many mitotic figures. The cells of the ventral root are doubtless medullary cells migrating directly along the motor fibers, while those found along the dorsal root arise from spinal ganglion cells. At the ventral border of the myotome the motor and sensory neurocytes group into cellular clusters which are the primordia of the sympathetic ganglia; no cranial sympathetic can be found yet. At

6 mm. the spinal nerves become fibrillar but numerous neurocytes are still migrating along them. These neurocytes keep their round aspect while others look more and more elongated so as to become sheath cells. At the ventral border of the myotome the neurocytes migrate toward the lateral angles of the aorta where they form the sympathetic ganglia connected with the mixed spinal nerve by the communicating ramus. The first three spino-occipital nerves have no dorsal roots, having only a small anterior root with a rudimentary sympathetic cluster. At the stage of 7 mm. the communicating rami of the last two spino-occipital nerves and those of the first seven spinal nerves are mostly atrophied. From the eighth to the fifteenth spinal segment, besides the ramus existing at the preceding stage, a new communicating branch has appeared, purely cellular, situated more dorsally than the primary one, nearly parallel to it but entirely independent. The ciliary ganglion has developed by cellular elements migrating along the ophthalmic branch of the trigeminal nerve and by others following the fibers of the oculomotor nerve. In embryos 9 to 9.5 mm. the trunk sympathetic system is almost identical with that found in the preceding stage. The peripheral part of it is much more developed, the sympathetic trunks being followed very near to the anlagen of the interrenal organ. Between this stage and the 10 mm. one, the sympathetic chains have grown very extensively in the cranial and caudal directions. Cranially it has acquired very intimate relations with the vagus nerve and at the level of the first spinal nerve it shows a direct anastomotic branch to the vagal ganglion, which might suggest an exchange of cellular elements between the two trunks. The first seven spinal nerves do not show any trace of communicating ramus. From the

eighth segment on, besides the secondary ramus a tertiary one has appeared. It is a very short branch, at once fibrillar, terminating in a new cellular heap, the secondary or vertebral sympathetic ganglion, distinct from the primary or aortic ganglion. The secondary sympathetic ganglia soon become united to each other by commissural branches and to the corresponding primitive ganglion by a small fibrocellular tract. The secondary or vertebral sympathetic ganglia are derived from migratory neurocytes of the corresponding spinal ganglion. They appear as direct extensions of the spinal ganglia and no contribution from the spinal cord by way of the ventral roots is to be found.

In the development of the sympathetic system in birds, a few details are worth mentioning. In chick embryos from three to four days of incubation, the mixed spinal nerves are already formed, the anterior root being mostly fibrillar, the posterior one cellular. At the basal part of the anterior root numerous neurocytes, doubtless originating from the medullary tube, are grouped into a small cellular cluster from which cells detach themselves to migrate along the motor fibers and to mingle with the migrating elements derived from the spinal ganglia. The primary sympathetic chain disappears and as in reptiles is followed by the differentiation of a secondary one. Soon after this moment, the peripheral sympathetic nervous system is formed by the growth of periaortic fibrocellular trunks, of which branches are going to the kidneys, adrenals, gonads and anterior part of the intestine. The posterior part of the intestine is innervated by the nerve of Remak, itself originating from the periaortic plexus at the level of the gonads and of the adrenals. From the cervical part of the primary sympathetic chain a few branches anastomose with the branchial ganglion of the

vagus nerve, and they very probably represent the source of the sympathetic elements which by the way of the vagus nerves migrate toward the lungs, the heart and the oesophagus. The cranial sympathetic system is represented by the ciliary ganglion and the cranial extension of the primary and secondary trunk sympathetic chains. The superior cervical sympathetic ganglion is located near the glossopharyngeal and vagal ganglia, with both of which it is connected by anastomotic branches.

In mammals also Ganfini ('18) describes the double origin of the sympathetic ganglia, from medullary elements migrating along the motor roots and from spinal ganglion cells. In the cervical region the communicating rami are purely cellular. They disappear very quickly, and the cervical sympathetic chain remains without any direct connection with the cervical spinal cord. In the thoracoabdominal region the primary sympathetic chain is first lateral to the aorta, becoming ventral to it at a later stage. At the moment of that change in position, new neurocytes accumulate in a longitudinal cord located at the dorsolateral angle of the aorta, representing a true secondary chain. The two chains are very near each other, in some places in direct continuity. When they have received their total supply of migrating neurocytes, the primary cellular communicating rami are replaced by new fibrillar connecting branches to the secondary sympathetic chain, a small twig remaining in direct relation with the primary ganglion which has migrated, ventrally. Ganfini is inclined to admit that while the primary sympathetic ganglia contain elements migrating along both roots, the secondary ones derive exclusively from cells of the spinal ganglia.

These careful observations of Ganfini are extremely interesting, showing that a

common scheme may be applied to the development of the sympathetic chains in all the series of vertebrates, except the selachians. The chronological succession of two generations of sympathetic elements is found in all groups with some variation concerning the details of their arrangement. The double origin of the primary elements, as opposed to the spinal ganglion origin of the secondary ones, is an entirely new idea, the importance of which is not to be lessened and which might explain a goodly number of divergent observations. One might regret that the earliest stages studied by Ganfini in reptiles, birds and mammals were already too old as far as the primary origin of the sympathetic elements is concerned. His observations do not eliminate the possibility that the cells found along the ventral roots may derive from the spinal ganglia or even from the neural crest. We know that in the development of the chick the stage of three days and twelve hours is already a very old stage as far as the primary sympathetic chain is concerned.

We have now to review the work of A. Kuntz, whose very numerous publications dealing with the sympathetic nervous system in various series of vertebrates represent the most extensive investigations ever carried on in this field from the embryological standpoint. We shall follow the chronological order and shall take each paper as basis for a comparative discussion of the numerous observations hitherto reported.

In 1909 he studied the rôle of the vagus nerve in the development of the sympathetic nervous system in pig embryos. This paper is in fact the basis of Kuntz's theory and deserves some attention. In a 6-7 mm. pig embryo the vagus nerve does not extend beyond the level of the heart. In the walls of the stomach the paths of the vagus branches are indicated by the pres-

ence of numerous cells which are easily distinguished among the mesenchymal cells by their larger size and the characteristic chromatic structure of their nuclei. These cells show a tendency to spread into the entire gastric wall until they have completely surrounded the stomach. Similar cells are found scattered in the walls of the intestine throughout its length as if, once having reached the anterior region of the digestive tract, they were able to migrate posteriorly all along its course. That those migrant cells found in the intestinal wall have wandered out from the vagus trunks can not be doubted. It is impossible to trace them to any other sources. There is no evidence of ventral migration of cells from the ganglia of the sympathetic trunks in the regions of the oesophagus or of the mesentery, except the fact that in the regions where later the coeliac and hypogastric plexuses develop a few sympathetic cells can be traced to the ventral aspect of the aorta. At 12 mm. the vagus branches can be followed to the lesser gastric curvature. There exist neither cellular nor fibrillar connections between the sympathetic trunks and the intestinal wall. These connections do not appear before the stage of 16 mm. and not until then do numerous sympathetic cells wander down into the myenteric and submucous plexuses. The anlagen of the pulmonary and cardiac plexuses originate evidently from cells wandering from the vagus trunks. The coeliac, renal and hypogastric plexuses arise from the sympathetic trunks and are easily seen in 10 mm. embryos, forming somewhat continuous fibrocellular masses. As far as concerns the primary origin of the elements forming the sympathetic anlagen, he describes a cellular migration into the ventral roots, with a later contribution from the spinal ganglia along the dorsal roots. This description is in fact the review of three

different papers published the same year and represents the type of Kuntz's descriptions of the histogenesis of the autonomic nervous system in mammals.

It might be remarked that in a 6-7 mm. embryo in which the vagus trunk is still behind the heart, Kuntz describes vagal-sympathetic cells not only in the stomach but also in the intestinal wall and that he accepts their vagal origin mostly because he does not see any other origin. Since those cells do not present any direct continuity with either the vagus or the sympathetic trunks, we do not see any serious reason to admit the first origin rather than the second one. A mesodermal origin, in the conception of Tello, might just as well be considered. Concerning the primary origin of the sympathetic elements, no definite conclusion could be drawn as to the origin and destination of the cells found along the ventral roots. Harrison ('01) was one of the first to suggest that the few medullary cells found along the ventral roots of *Salmo* might contribute to the formation of the sympathetic primordia. The many other workers who described those migrating medullary cells did not make a careful distinction between true medullary cells migrating out of the spinal cord and cells found along the motor roots. Cells may be described just outside the external membrane and yet result from a migration towards that region. Kuntz's figures in particular probably deal with this second cellular type, especially since his stage of 6-7 mm. is very evidently too old. The mixed nerves are formed and covered with sheath cells. The sympathetic elements have already migrated near the dorsolateral angle of the aorta.

Kuntz ('10) next investigated the development of the sympathetic system in birds. He verified the old description by His of the succession of two sympathetic

chains, the primary system existing from the fourth to the sixth day; the permanent one beginning its development during the sixth day. The prevertebral plexuses originate entirely from the primary sympathetic trunks. They are already clearly defined at the end of the fourth day with a direct cellular continuity between them and the primary chain. Sympathetic cells in very great abundance can be followed to the anlagen of the adrenals. At the end of the sixth day the majority of the elements of the primary trunks have migrated into the prevertebral plexuses. From these plexuses, however, neither cells nor fibers extend more ventrally, except in the sacral region, where from the hypogastric plexus numerous cells migrate toward Remak's ganglion; the latter can be observed from the fourth day on. The ganglion of Remak has no corresponding structure in mammals, but in reptiles, especially in turtle embryos, numerous ganglionic masses can be observed dorsally to the rectum, representing doubtless the prototype of Remak's ganglion. In a 130 hour chick embryo the vagus trunks are found along the walls of the oesophagus, the vagal ganglia being located very near its lateral walls. In front of the bifurcation of the trachea, numerous vagal cells wander out into the oesophageal wall, being very poorly differentiated and difficult to distinguish from the surrounding elements. At the end of the sixth day those migrating cells have formed a double ring around the oesophagus. The plexuses in the intestinal region appear only during the seventh and the eighth days, but Kuntz was unable to observe their origin clearly. There is no evidence of any penetration of cells from the sympathetic trunks or the prevertebral plexuses. Many cells probably arise from Remak's ganglion by a forward migration. Still he considers that a posterior migration of vagus cells must

represent the most important contribution. This last conclusion looks rather an audacious one and is not supported by any valid argument. To recall an analogy with histogenesis in mammals is far from bringing any evidence.

The histogenesis of the sympathetic nervous system in amphibians was studied on embryos of frog and of *Amblystoma* ('11). The sympathetic elements in this group obviously wander from the spinal ganglia or perhaps from the neural crest. The cells can easily be traced from the distal end of the spinal ganglion to the lateral aspect of the aorta. There is very little evidence of any migration of medullary cells in the ventral nerve roots, and Kuntz establishes a correlation between this fact and the small amount of sympathetic elements existing in embryos of this group. The myenteric and submucous plexuses are very difficult to recognize and their development could not be traced with great accuracy. In spite of this fact Kuntz considers that his preparations leave no doubt as to the genetic relationship of these plexuses to the vagus nerves and that no other origin could be traced.

The study of fishes ('11) shows very interesting details. In 6 mm. embryos of *Acanthias* the spinal ganglia are not yet differentiated. The neural crest cells may be observed along the lateral aspects of the neural tube. Numerous medullary cells are pushing out of the cord into the growing ventral roots. At 7.8 mm. in length the neural crest cells migrate beyond the ventral level of the neural tube, while numerous medullary cells still follow the ventral root fibers. The cells of both sources become scattered in the mesenchyme and show a tendency to concentrate at the dorsolateral angle of the aorta. It is very easy to distinguish the two cellular types. The neural crest cells have a much larger nucleus than the med-

ullary cells. At 10 mm. the spinal ganglia are definitely differentiated, and from their distal poles numerous elements are migrating along the dorsal root. The motor roots have become fibrous, although a few medullary cells can still be observed pushing out of the neural tube. The migration in the dorsal roots goes on for a considerable period of time; the wandering cells being still scattered in the retro-aortic mesenchyme. The aggregation of these elements takes place only at the stage of 13 mm., but at this moment the motor and sensory bundles are not fused but situated near each other, so that the sympathetic primordia show connections only with the sensory root. Neither the spinal ganglia nor the neural crest may be looked upon as the sole source of the elements contributing to the formation of the sympathetic system. An important part doubtless originates in the ventral half of the neural tube. The wandering of sympathetic cells seems to be the result of the attractive action of hormones which are produced by the cellular elements in the highly vascularized regions. This could explain the migration toward the aortic region and toward the cardinal veins. As far as concerns the myenteric and submucous plexuses no clear figures of their development could be observed, owing to the fact that the intestinal wall becomes muscular before the development of those plexuses. He feels that the vagal origin is the only possible one.

In a 4 mm. embryo of *Amia calva* numerous cells migrate ventralward from the spinal ganglia, while there exist no clear pictures of medullary cells wandering along the ventral roots. Migrating cells are only found at 8 mm.; it might be recalled that Ganfini described them at the stage of 6 mm. The selachian material has been studied by Müller, and we have

seen the quite different interpretation given by him.

In his other papers dealing with the development of the sympathetic system in man ('20), in the turtle ('11), or with general applications to the series of vertebrates ('21), Kuntz does not add any new facts. The same theories are presented and the same critical considerations apply to all of them.

The first experimental attempt was realized by Kuntz and Batson ('20) on chick embryos. In seven chick embryos of 48 hours of incubation, they destroyed the dorsal half of the nervous system in a few segments, by the electrocautery method. In spite of this destruction, four or five days after operation they found a normal disposition of the sympathetic trunks as well in the injured region as in the remaining part of the embryo. Their conclusion was that the migration of the sympathetic cells from the neural tube seems to be accomplished along the ventral spinal roots.

Kuntz ('22) published another paper based on experimental researches in chick and frog embryos. The chick material is to a great extent the same as he described in the first publication, and we shall not discuss it for the moment. Various operations were performed on frog embryos, such as removal of the neural crest and dorsal half of the nervous tube, extirpation of the entire spinal cord and removal of the medulla. The animals were allowed to develop isolated, or two animals were healed together. They all show a markedly slowed development. Complete removal of the spinal cord prevents the development of the sympathetic Anlagen. These are thus genetically related to the cerebrospinal nervous system, as is admitted by most workers. Embryos from which a strip of tissue including the neural

crest and the dorsal half of the neural tube was removed, show three or five days later a complete absence of spinal ganglia and dorsal nerve roots, while the ventral roots accompanied by medullary cells and the primordia of the sympathetic trunks are present in all segments providing an important amount of nervous tissue is left intact. As far as concerns the visceral plexuses, the frog embryos in which he removed the medulla did not live a sufficient period of time to allow definite conclusions.

Complete removal of the neural tube in chick embryos from the lower cervical to the sacral region prevents the development of the sympathetic trunks and of the prevertebral plexuses in the lumbar region. In the thoracic region the operation was incomplete on one side. In these operated embryos the primordia of the oesophageal, pulmonary, cardiac and enteric plexuses are present and apparently contain as many cellular elements as in unoperated embryos of five days of incubation. Inversely, in one embryo he successfully destroyed the hindbrain. It was found dead five days later. The microscopic study showed normally developed sympathetic trunks and prevertebral plexuses, while the primordia of the pulmonary, cardiac and enteric plexuses were entirely lacking.

This experimental work of Kuntz represents a very interesting attempt to discriminate the real source of the sympathetic elements and the constitution of the visceral plexuses. There are, however, a few objections which might be formulated against his interpretations. Concerning the primary origin of the sympathetic elements in frog embryos his deductions are not at all convincing; his figures are poor and the so-called migrating medullary cells in the ventral roots may just as well be considered as mesenchymal cells. He furthermore did not

make a careful search for isolated ganglion cells or Rohon Beard cells. The careful piece of work of Müller and Ingvar, corroborated by the descriptions and the experimental results of Harrison, seems of much greater value. Harrison admits some migration of medullary cells along the ventral roots, but he considers that they probably become sheath cells. They are very few in number, and the experimental evidence of their existence was only observed twice in the experimental series.

If we consider the same question in chick embryos, we are also not convinced of the soundness of Kuntz's conclusion. The operations were always incomplete, the described result being found only in a few segments or on one side. That means the possibility of a direct extension from the adjacent segments or from the other side of the embryo. We do not know the exact morphological stage of development at the time of the operation; the number of hours of incubation is too inaccurate a way of determination on account of the very great variations occurring in a group of eggs placed in the incubator at the same moment. The result of this last consideration is that we do not know whether or not any migration of neural crest material occurred before the operation. Electrocauterization is a blind way of doing experimental embryology; in using this method it is practically impossible to localize the lesion exactly and to determine its extent.

If we consider the second point of Kuntz's theory, the rôle of the vagus nerve in the constitution of the so-called vagosympathetic plexuses, we find only one embryo in which he removed the vagus nerves successfully. Unfortunately the embryo was found dead after a total incubation of five days. It is doubtful whether, according to the morphological description of normal embryos given by

Kuntz himself, this embryo would be old enough to show the enteric plexuses and whether the post mortem alterations as well as the progressive death of the embryo did not make very uncertain the identification of those plexuses.

Taken as a whole, the experimental part of the researches of Kuntz is by no means conclusive. The immense interest of this research is the fact that Kuntz was the first investigator to apply experimental methods to the embryology of the sympathetic nervous system. Müller and Ingvar repeated the same experiments a few years later with quite different results, and we willingly would give more weight to their work because of an apparently

cleaner experimental procedure. However, the question remains entirely unanswered and further researches will be needed. Detwiler ('29) throws a doubt on the interpretation of experimental results after the removal of the neural crest. In three *Amblystoma* embryos in which he removed the neural crest by a complete scraping at the tail bud stage, well developed spinal ganglia were found. He admits a complete regeneration of the neural crest. It would be very important to know what was the dorsal limit of the operations, in order to determine the exact source of the new forming neural crest.

(To be concluded)





LIVING WATER

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INTRODUCTION

WATER is the chief chemical constituent of most living organisms. Being the medium in which the majority of the other constituents live and move, its presence is more often taken for granted than considered as a major regulation by the organism. For living substance is not merely endowed and kept; it is in communication with its surroundings. From its environment it continually or interruptedly takes up new materials, and to its environment it gives up some of what it had. Whether all such exchange is necessary, or whether some is accidental to the preservation of normal functioning, can hardly be decided experimentally.

The vortex of vital activities is with respect to water more than analogous to the whirlpool. Without water both the body and the pool would be but paleontological specimens, showing only (in Huxley's phrase) where activity has been.

In studying the various constituents of living organisms, it is customary to refer their quantities to that of water. Contents are expressed therefore as concentrations. But the content of water can hardly be so expressed. In many investigations water is represented as wet weight minus dry weight. This conveys little of physical or physiological significance, except in the case of direct and immediate comparisons. Somewhat more informing are determinations of total osmotic pressure and its various correlatives. These

values are useful because they measure one of the forces which control the exchanges of water among tissues.

RATES OF TURNOVER OF WATER

The most important measurement concerned with water balance is the rate at which water is continually passing into and out of body or tissue. In organisms which have definite paths of assimilation and dissimulation, to measure the rate is a feasible procedure; and some of the results obtained are listed in table 1. Further data exist upon other species (56), particularly of marine fishes (24).

In man practically all assimilation is from the alimentary tract, and all elimination is through the urinary tract, the skin, and the lungs. In the frog all intake is through the skin; the output which can be measured is through the cloaca. To tell how much fluid passes both in and out through the skin is no more possible than to tell how many molecules of water pass through an osmometer only to be instantaneously counterbalanced by an equal number moving in the opposite direction. In the earthworm a still smaller proportion of the total water exchange can be actually measured, namely that which is eliminated through the anus. Finally in *Ameba*, where the volume of contractile vacuoles only is measured, it is likely that only a few per cent of the total exchange of water are actually detected. The values given in table 1 are, therefore, the lower limits of the actual turnovers.

Comparative rates of excretion have been analysed by Pütter (56) to demonstrate that among various species of animals the rate of water output is inversely proportional to the cube root of the body weight, *i.e.* to the linear dimension. Much more accurate data are required to make this generalization significant.

It is obvious that there is for each species a tremendous range of turnover rates, within which the water content of the organism may remain constant. What is required for normality is that the intake and output shall be equal. Thus, a frog may be taken from water and put in an

TABLE 1

Rates of turnover of water, expressed as per cent of body weight per 24 hours, at about 20°C.

SPECIES	MODE	MINI-MUM	MAXI-MUM	REFERENCE
Man.....	3.4	1.4	68.0	(1)
Frog.....	31.0	<5.0	93.0	(12)
Earthworm.....	19.0	1.0	>30.0	(9)
<i>Ameba</i>	520.0	<75.0	>615.0	(6)

atmosphere nearly saturated with moisture, when no water will be absorbed, and practically none excreted (12). But the individual tissues are none the less in their normal state. If a man drinks water as fast as his alimentary tract will absorb it, the kidneys will excrete it about as fast as it is absorbed. Yet the dilution of the blood is so small that it can be detected only by a few very precise methods (55).

A comparison of the turnover of water with that of other substances shows that in man water occupies a high place. Whereas (table 2) nitrogen is replaced in the human body only every 290 days on the average, water holds its position in the body only twenty-one days. It is most nearly rivalled by sodium chloride; this is due more to dietary habits than to

necessity. Obviously, water has this unusually high rate of turnover because it is the substrate, the solvent and conveyor, for all other substances. In birds, where probably less exchange takes place through the skin, and where even urinary water is reabsorbed, water has a relatively low rate of turnover. But in freshwater animals such as frog, earth-worm, and *Ameba*, the turnover of water is very far above that of all other substances com-

TABLE 2

Average rates of turnover of each chemical element in a 70 kilogram man. Most of the data from which this table is drawn up are contained in the book of Sherman (63)

ELEMENT	BODILY CONTENT	DAILY REQUIREMENT	DAILY REQUIREMENT AS PER CENT OF CONTENT
	gm.	gm.	
C.....	12,600	250.0	2.0
O.....	45,500	3350.0	7.4
H.....	7,000	350.0	5.0
N.....	2,100	7.13	0.34
S.....	175	0.68	0.39
P.....	700	0.88	0.126
Ca.....	1,050	0.45	0.043
K.....	245	3.40	1.39
Na.....	105	1.95	1.86
Mg.....	35	0.34	0.97
Fe.....	3	0.01	0.33
Cl.....	105	2.85	2.71

bined. In marine animals (24) the rates of water turnover appear to be less than in freshwater ones; in them all intake is probably through the alimentary tract.

The metabolism of water therefore depends upon its availability in the environment. But it depends also upon a number of other factors, such as the ability of the body to conserve water, as against dehydrating forces; the bulk and surface of the body; and the various phylogenetically determined properties of the body and its tissues.

WATER EXCHANGES OF FROGS

The organism whose exchanges of fluid with the environment have been studied most extensively is the frog. But there are differences among various species of frogs, and the description may therefore be limited first to adult *Rana pipiens*.

such an experiment are indicated in figure 1.

The rate of accumulation of urine turns out to be proportional to the bulk of the body, and at 20°C averages 1.3 per cent of the body weight per hour, or 31 per cent per day (12). This amount of fluid is

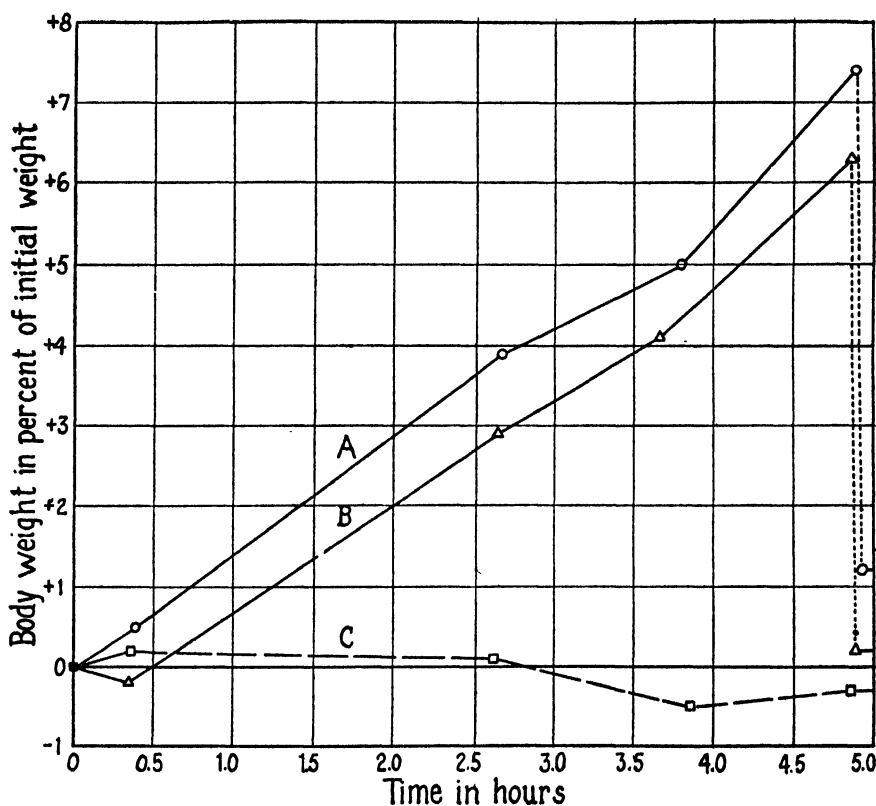


FIG. 1. PROGRESSIONS OF BODY WEIGHT IN 60-GRAM *RANA PIPIENTS* KEPT IMMERSSED IN TAP WATER

A and B were bound at the cloacae at zero time; C was not bound. At about 4.9 hours the cloacae were unbound, allowing the urine which had accumulated in the bladder to escape. The slopes of the lines A and B therefore are the rates at which water passed inward through the skin.

When immersed in tap water or distilled water, frogs are, of course, in dynamic fluid equilibrium, as is indicated by the fact that body weight is relatively constant. That the equilibrium is dynamic is shown by binding the cloaca with thread, when urine is forced to accumulate in the bladder. The results of

continually passing in through the skin, for unfed frogs never ingest water by mouth. At any other temperature a balance is likewise struck, though the rate of passage of fluid is increased about 2.3 times for each increase of 10° in temperature.

The rate of fluid turnover may also be

varied by placing frogs in diverse solutions. In various concentrations of sodium chloride up to 0.15 osmolar, the rates of urine formation are equal to that in tap water, but are smaller in higher concentrations, so that above 0.22 osmolar the rates are constant at only 5 per cent of the body weight per 24 hours (12).

Placing the frogs out of water in an atmosphere saturated with moisture stops urine formation. The view may be taken that the rate of water excretion depends directly upon the availability of water within the body. Temperature and concentration therefore affect water intake primarily; water output adjusts itself to the conditions then existing in the body. If water or a solution is injected into the body, then the kidneys eliminate this fluid over and above the amount which is being brought into the organism by the skin (12).

The frog thus regulates its fluid content chiefly at the output and not at the intake. This is the case in man and most other organisms which have been studied. The chief difference between freshwater organisms and man is that the former are ordinarily forced continually to take up fluid from the medium; while terrestrial species can deny or satiate themselves.

FORCES CONCERNED IN WATER EXCHANGES OF FROGS

Experiments with isolated frog skin demonstrate that this continual inward passage of water does not depend entirely upon the fact that the concentration of substances is greater inside the body than outside it. The skin may be reversed in orientation, when the rate of passage of water from the medium to Ringer's solution is many times faster than in the normal orientation (4). An experimental analysis of the forces concerned in the passage of water therefore becomes necessary.

Owing to the great irregularities found in measurements of fluid migration through isolated skin, the chief observations must be carried out upon living frogs.

The rate of any movement of water must be proportional to the forces producing it. These forces may include gravity, friction, tissue tension, osmotic pressure, electrical potential, and a number of others. The problem is to evaluate each force as independently of others as possible, in order to ascertain the quantitative rôle of each one.

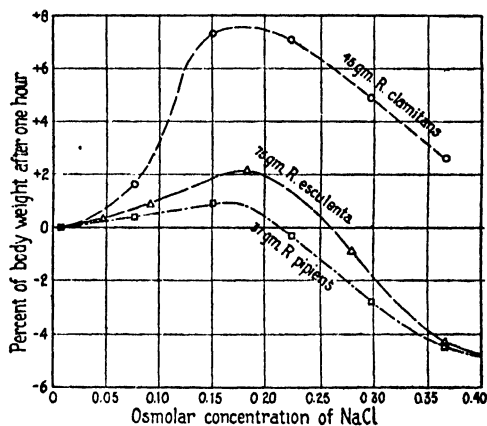


FIG. 2. INITIAL RATES OF NET WATER ACCUMULATION OR LOSS IN THREE SPECIES OF FROG

The average weight of one individual is indicated. The points for *Rana pipiens* and *Rana clamitans* are each the average of about 30 individuals. The points for *Rana esculenta* are for single individuals and are taken from Durig (18).

In frogs, osmotic pressure can be evaluated by placing individuals in various concentrations of medium, and noting the initial rates at which water is gained by the body (8, 13). Such a curve, in which each point represents the average result on about 30 individuals, is shown for *Rana pipiens* in figure 2. To give the rate of passage through the skin, this curve needs to be corrected for the accumulation of urine. The shape remains the same after correction, the rate of inward passage of

water being greatest at 0.16 osmolar concentration.

Osmotic pressure alone would cause an initial movement of water which is proportional to the gradient of concentration. It follows that the exchanges of water which begin when the frogs are put into the various concentrations of sodium chloride are caused in large part by forces

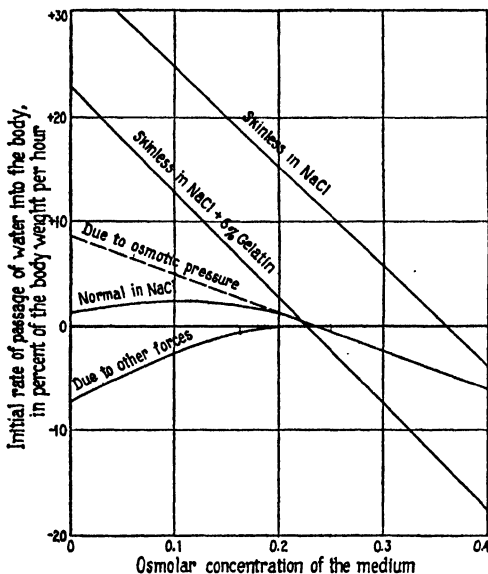


FIG. 3. COMPARISON OF THE RATES OF PASSAGE OF WATER INTO 37-GRAM RANA PIPPIENS IN RELATION TO CONCENTRATION OF SODIUM CHLORIDE OF THE MEDIUM

Each curve is the smoothed average result for many frogs. The curve "normal in NaCl" represents the rate of passage through the skin of intact frogs having the cloacae bound so that urine could not escape.

other than osmotic pressure (13). Only in the higher concentrations, where the medium is more highly concentrated than the frogs' blood and lymph, do the rates of exchange of water give any appearance of being proportional to concentration.

The rôle of the skin may be distinguished by means of a parallel series of experiments in which the frogs have their skins removed, and are immediately placed in various concentrations of sodium chlor-

ide (15). These frogs are alive, maintain their circulations for at least an hour, but have their muscles, blood capillaries, and other tissues in contact with the medium. The initial rates of net water exchange are now proportional to concentration; the smoothed line for them is shown near the top of figure 3. The skinless frog appears to be an ideal osmometer.

But the difficulty may be noted that the skinless frog gains weight in concentrations up to 0.36 osmolar, which are much higher than the total concentration of the blood. The intact frog, on the other hand, neither gains nor loses water in about 0.23 osmolar, which is equal to the total concentration of the blood and lymph. It is possible that this peculiarity of the skinless frog is due to the absence of proteins from the medium. Another series of experiments with 6 per cent gelatin added to the medium of various concentrations of sodium chloride, shows this surmise to be correct. The concentration at which weight is neither gained nor lost, which might be considered an "isotonic" point, is now about 0.23 osmolar (figure 3). The difference between the solutions without and with gelatin is not due merely to the extra osmotic pressure of the gelatin, which at most amounts to 0.02 osmolar, but to the ready passage of sodium and chlorine into the tissues except when the skin is present.

Without the skin, all the other forces at work are evidently constant, so that only osmotic pressure exerts its effect. The slope of the line showing rates of migration of water into skinless frogs at various concentrations, is about 2.6 times greater than the slope of the line for normal frogs in the higher concentrations (figure 3). It is likely that this is due entirely to the smaller distance through which water has to diffuse in order to enter the circulation of the skinless indi-

viduals. Assuming this to be the case, we arrive at the probability that the slope of the line in higher concentrations for intact frogs represents the rate at which water would be entering or leaving the frog's

that of the medium. The data upon which this statement is based are shown in figure 4.

All other forces present can now be evaluated by merely taking the difference

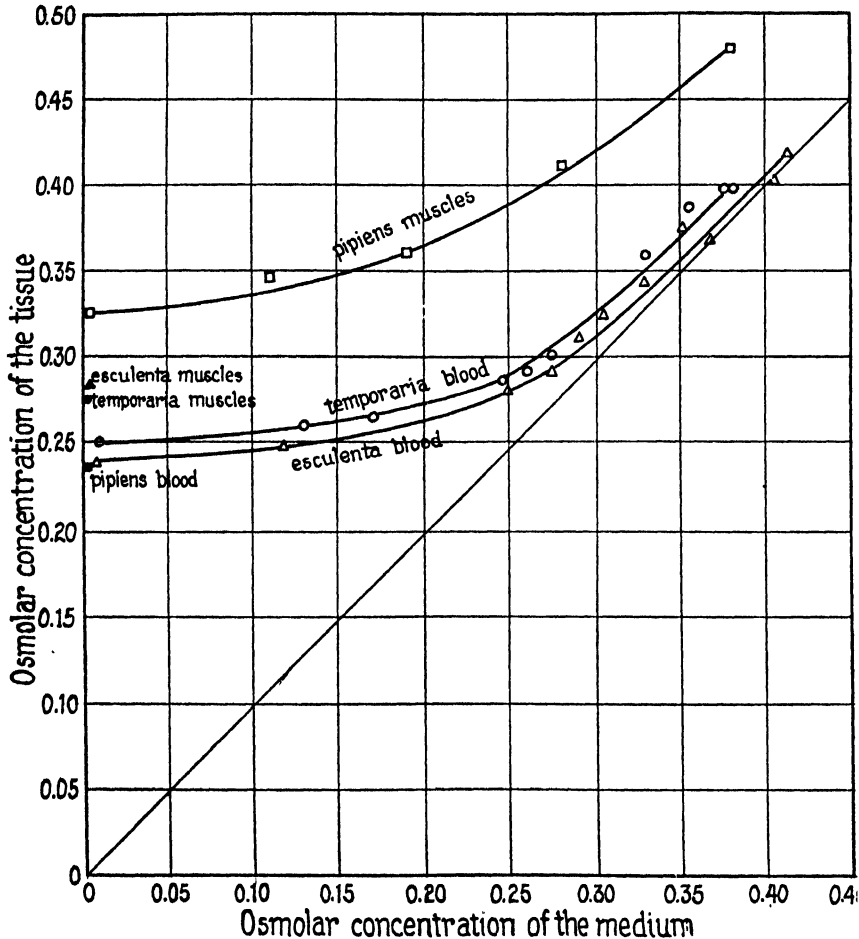


FIG. 4. EQUILIBRIUM OF OSMOTIC PRESSURE OF DEFIBRINATED BLOOD, OR MUSCLES, OF THREE SPECIES OF FROG IN MEDIUM OF VARIOUS CONCENTRATIONS OF SODIUM CHLORIDE

The data are for: Esculenta blood (22, 23); Temporaria blood (31); Pipiens blood (46); Esculenta muscles (34); Temporaria muscles (17); Pipiens muscles (13).

body if there were no forces active except the one of osmotic pressure (15). This probability is rendered almost certain by the fact that after twenty-four hours in any *hypertonic* medium the osmotic pressure of the blood is very nearly equal to

between the extrapolated value for the movement of water due to osmotic pressure, and the actual value found. These forces are significant in amount only in *hypotonic* concentrations of the medium. Further identification of the nature of

these forces, which reside wholly in the skin, cannot at present be made, though various possibilities have been tested through correlative studies of oxygen consumption (14), electrical potential, and temperature coefficient in relation to solutions.

The skin of a frog is a boundary through which water is exchanged much as it is exchanged through any other membrane. But in this boundary are situated forces which are not encountered in all membranes; and these forces vary in amount with many sorts of changes in the internal

vidual has remained in a given medium (13). For this reason if for no other it is not surprising to find that different species exhibit diverse responses upon being transferred to new concentrations of medium.

Four species of *Rana* have been tested in relation to concentration. Among these four the curves for rates of water exchange are roughly similar in shape; but very significant differences in magnitude are present. Three of these four are shown in figure 2; the curve for *Rana temporaria* (17) or *Rana fusca* (68) is nearly identical with the curve for *Rana esculenta*,

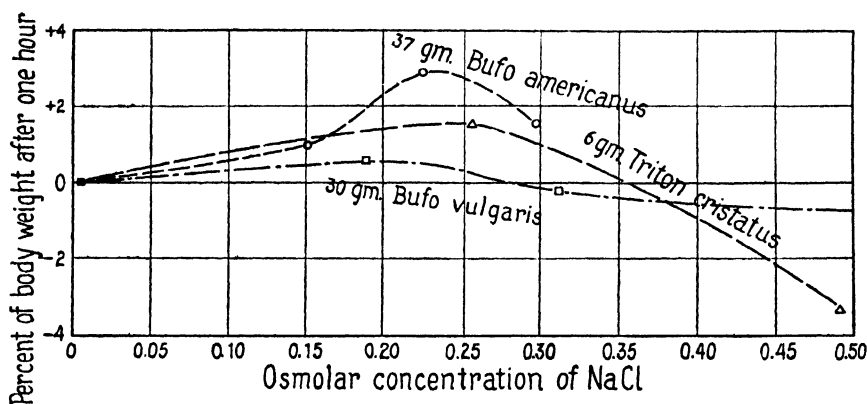


FIG. 5. INITIAL RATES OF NET WATER EXCHANGE IN ONE SPECIES OF SALAMANDER AND TWO SPECIES OF TOAD
The points for *Triton cristatus* and *Bufo vulgaris* were obtained on single individuals by Backman and Sundberg (17).

and external environments of the animal. The skin is not a mere "sieve," or "semi-permeable," or possessed of "one-way permeability;" instead it is the seat of certain forces which modify the exchanges of water in compliance with conditions. It is possible that the permeabilities of all kinds of membranes can be evaluated by similar procedures in terms of the forces present.

WATER BALANCE OF VARIOUS AQUATIC ORGANISMS

It is found that the intensities of the forces which reside in the skin of *Rana pipiens* vary with the time that the indi-

Only three other species of amphibia have been studied in relation to concentration of the medium. As shown in figure 5, *Triton*, a urodele, qualitatively resembles *Rana pipiens*, but the concentration at which its weight remains unchanged is much higher. The difference between the two species of toads, *Bufo*, which have been studied, is striking. It is certain that toads are not terrestrial organisms from the point of view of their water balance, for they exchange water through the skin equally rapidly with frogs, and they evaporate just as fast through the skin when taken out of water.

The larvae of amphibia differ from the

adults of the same species in their water balances when placed in diverse concentrations of the medium. *Rana pipiens* behaves very like the ideal osmometer at all ages from soon after hatching up to metamorphosis, as shown in figure 6. Upon the day at which it ceases to use its gills for respiration it changes its water exchanges to those characteristic of the adult (11).

Tadpoles of other species of *Rana* may differ significantly, as is the case for *Rana temporaria* (figure 6). Larvae of *Amblystoma*

and earthworms may be judged from their initial exchanges in solutions of sodium chloride to be freshwater organisms of the type resembling the ideal osmometer (5, 9). But it is also true that in course of time they, and many other of the species mentioned above, acquire or exert forces which overcome the one of osmotic pressure. It is also obvious that another force must be ever present when these animals are in the initial or usual state, for their internal media are always more concentrated than the fresh water in which they live.

Three unicellular species have been studied in relation to concentration of the medium (27, 33). In each species the initial exchanges upon transfer to various concentrations are similar to those for the earthworm.

Among marine invertebrates the exchanges of water in relation to concentration of medium have not been worked out systematically for any one species. Qualitatively it is always found that species belonging to several phyla gain body water in diluted sea water and lose body water in concentrated media (61, 57, 25, 26). Marine fishes appear also to obey this rule so far as the incomplete data go (66, 62).

Considerable information about the balance of water between organisms and environments is furnished by studies of the osmotic pressures of body fluids as modified by the concentration of the medium. Such data are available upon many marine species, for among them are a large number which can live comfortably in a wide range of concentrations, even in fresh water. Among freshwater species the range of species and of concentrations which can be studied is more limited.

When this correlation of body fluids and media is made, sufficient time for complete equilibrium having been allowed in

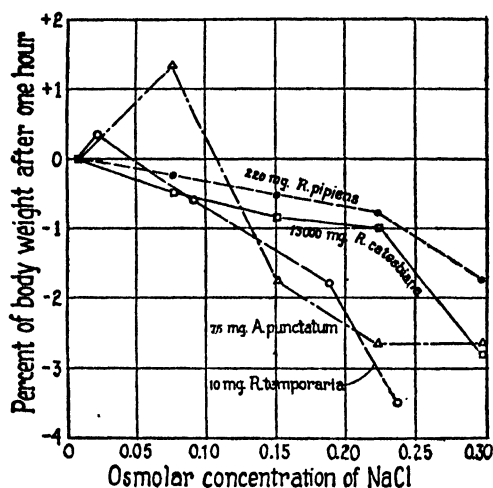


FIG. 6. INITIAL RATES OF NET WATER EXCHANGE IN FOUR SPECIES OF LARVAL AMPHIBIA (10)

Within a species the rates are less for larger individuals, but the shape of the curve is unchanged. The points for *Rana temporaria* are taken from Roaf (58).

punctatum show still another titration curve (10).

Among freshwater fishes the only curves which have been worked out do not resemble the curve in frogs (66, 45, 38). An illustration is *Gasterosteus* shown in figure 7. It is likely that still other types of curves will appear among fishes when more species have been studied in this particular manner.

Few invertebrate species have received study of the sort required. Planarians

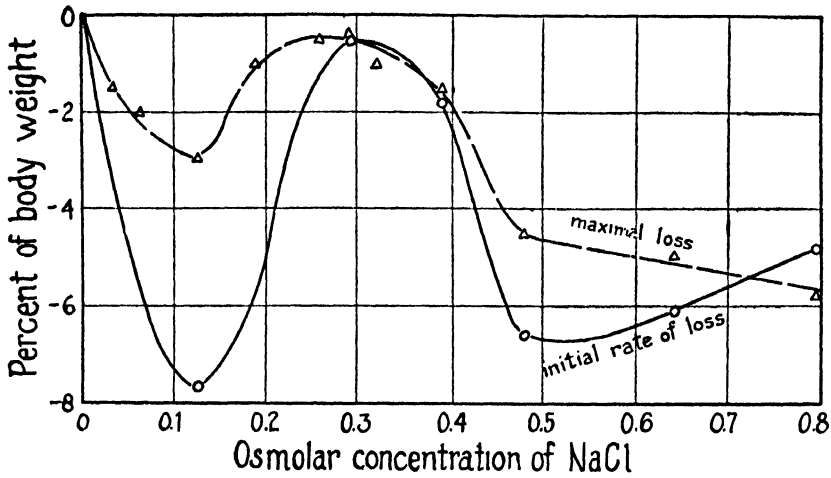


FIG. 7. LOSSES OF WATER BY THE FISH *GASTEROSTEUS LEUURUS* OF ABOUT 2-GRAM SIZE, UPON TRANSFER FROM TAP WATER TO VARIOUS CONCENTRATIONS OF SODIUM CHLORIDE

Initial rates are plotted as change of body weight per hour in the first half hour after transfer. Maximal losses are average values selected by the investigator. The data are from Gueylard (38).

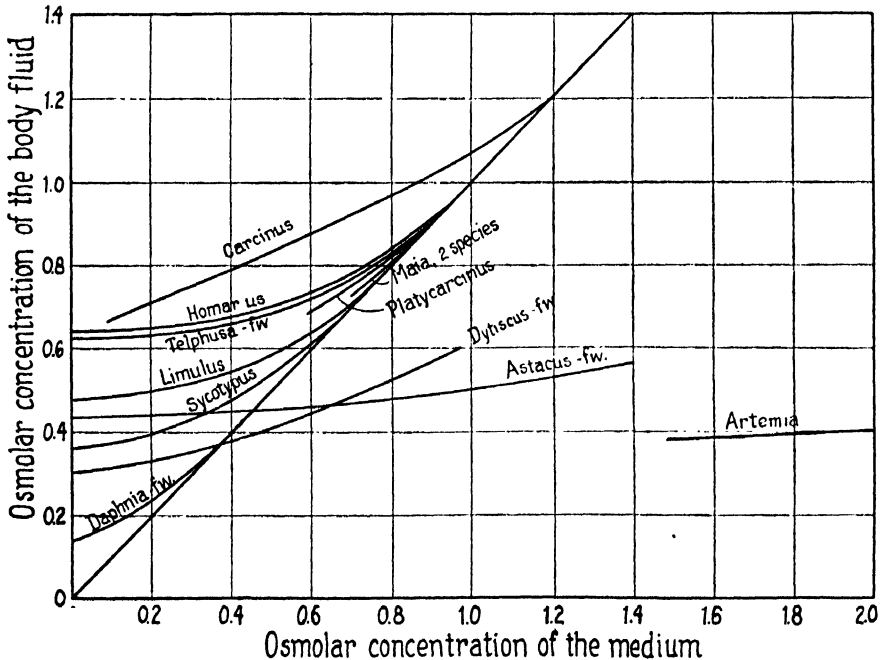


FIG. 8. EQUILIBRIUM OF OSMOTIC PRESSURE OF BODY FLUID OF VARIOUS SPECIES OF ARTHROPODS IN MEDIUM OF VARIOUS CONCENTRATIONS

The data are for *Carcinus* and *Maia* (35, 29), *Telphusa* (30), *Platycarcinus* and *Astacus* (29), *Homarus*, *Limulus* and *Sycotypus* (37), *Dytiscus* (16), *Daphnia* (36), *Artemia* (49). The four species marked "fw." normally live in fresh water.

every test, the various species fall into two groups. In one group there is equality of osmotic pressures at all higher concentrations, with progressive departure at lower concentrations in the direction of excess osmotic pressure in the body fluids. In the other group there is only a slight increase of osmotic pressure of body fluids over a large range of environing concentrations. The first group includes all invertebrates (with the exception of a few

maintain the osmotic pressures of their body fluids at almost uniform values whatever the concentration of the medium.

WATER BALANCE OF TERRESTRIAL ORGANISMS

Terrestrial animals are characterised by possessing integuments which retard evaporation to a huge extent, and which allow other water-exchanges only very sparingly.

Neither the earthworm nor any amphibian belongs to this type. But all reptiles and all the adult insects which have been tested are included in this category. *Phrynosoma*, *Alligator*, and *Chrysemys* when put in solutions of various concentrations exhibit no more exchange of water than when kept in water or put in air. The small species *Anolis*, however, shows significant changes of body weight upon transfer from water to solutions of sodium chloride; these changes are roughly similar to that for *Rana esculenta*.

In terrestrial plants, studies of water metabolism have concerned themselves almost exclusively with rates of loss by evaporation from leaves. It is found that the rates of root absorption ordinarily regulate themselves to keep pace with the leaf evaporation; the evaporation depends upon factors such as saturation deficit of air, surface of leaf, and size of stomatal apertures (41). But observations made over short periods of time show that there may be considerable lag in the uptake of water, especially upon treatment with certain solutions (53). In the usual daily cycle, the increase of transpiration at noon leads to a negative water balance throughout the afternoon. During the night water is then taken up to saturate all the tissues of the plant (41).

In any terrestrial organism the relative water content of the body is of course to be correlated not with the osmotic pres-

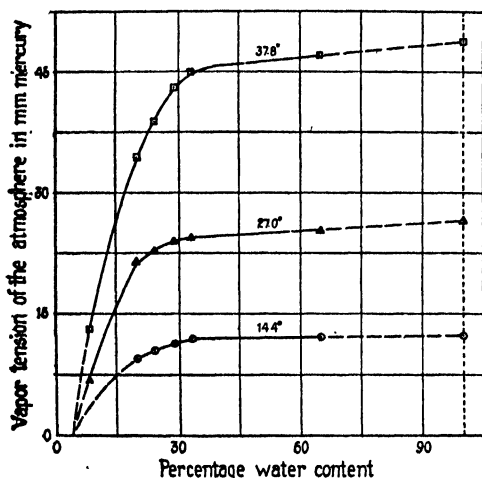


FIG. 9. EQUILIBRIUM OF WATER CONTENT OF THE MOSS *HYPNUM TRIQUETRUM* WITH THE VAPOR TENSION OF THE ATMOSPHERE, AT EACH OF THREE TEMPERATURES

The points plotted for 100 per cent water content are the saturation tensions of air in equilibrium with pure water, and these water contents of course were not found in the organisms. Redrawn from Mayer and Plantefol (48).

species of arthropods as shown in figure 8), the elasmobranchs, amphibia (see figure 4), and a few species of freshwater teleosts. The second group is characterised by the teleosts. The interchanges of fluid by all members of the first group must be qualitatively like those that have been described for the frog. The second group may include two kinds, those which do not interchange, as mammals, birds, reptiles, and some insects; and those which interchange substances freely, and yet

sure of a liquid medium but with the vapor tension of the atmosphere. This is the ideal information about water balance; it has been obtained in the case of only one species, the moss *Hypnum* (48, 54). The correlation between vapor tension and water content is shown in figure 9. It is plain that over a wide range, from saturation (at 65 per cent content) down to about 35 per cent content, the water content of the plant is directly proportional to the vapor tension of the atmosphere. It is unknown what specifically prevents supersaturation, that is, infinite dilution of the plant substance. Below 35 per cent content the curve of vapor balance is suddenly different, as though a new force were concerned in holding this water. At very low water contents, below 15 per cent, the forces which successfully resist evaporation are still stronger.

Figure 9 may be compared with figures 4 and 8. In the two latter the vapor tension of the body (which is inversely proportional to osmotic pressure) changes little over a considerable range of vapor tensions of the medium. In figure 9, on the other hand, it is the medium which changes little over a large range of water contents of the body. The frog is protected primarily against the entrance of too much water from the environment; the moss is protected against the loss of too much water to the environment. This contrast of equilibria with respect to water is probably the essential difference between the freshwater organism and the terrestrial organism; it is the secret of the successful survival of the one in pure water and of the other wholly removed from water.

The vapor tension curve for the moss is such that when its water content is as high as 60 per cent, water will leave a strong salt solution such as 2M potassium nitrate to go into the moss. If moss which has been equilibrated with pure water is put

into various strengths of potassium nitrate, its water content diminishes in proportion to the concentration, but only by about 3.5 per cent for 2M concentration. This amount of diminution corresponds roughly to the change of vapor tension in going from pure water to a solution of this strength in figure 9. Its exact evaluation is complicated by the fact that salt and water penetrate into the moss almost equally fast.

The equilibrium attained depends largely on temperature, as is shown in figure 9. But the velocity with which the equilibrium is approached is little influenced by temperature. Moreover, the equilibrium and the velocity are the same for moss which has been boiled at 110° as for living moss (54).

This study should point the way to fruitful experiments upon insects. It is well known that some insects will lose no water, and even gain in relative water content, during complete starvation and thirst (19). In a number of cases it has been observed that insects are able to absorb water from a humid atmosphere (21, 20) just as *Hypnum* does. In place of measurements of vapor tension of the atmosphere, the water content of wheat in and upon which certain weevils are living may be correlated with the water content of these weevils (59). The result is curious in that the weevils gained moisture as the wheat lost moisture, over a large range. This serves to call attention to forces and factors which are not present in the equilibria between solutions and atmospheres.

WATER BALANCE OF MAN

Man may be taken as the type of terrestrial vertebrate. His content of water is surprisingly constant from day to day, when it is considered that he loses, each 24 hours, five per cent of the quantity present (table 2). Not having an environ-

ment of water, it is necessary to take into the alimentary tract an adequate or an excessive amount. The behavior which is aroused through the sense of thirst appears normally to take care of this need. The main difference from the freshwater animal is that *all* the water in contact with the absorbing surface is absorbed into the circulation, for normally no sig-

end; so that absorption and elimination both go to completion without any measurable net retention or loss of body fluid.

By profuse sweating also it is possible to lose up to 2000 cc. of water per hour from the body (3). Could a man continue to ingest 2000 cc. per hour, he could either by diuresis or by sweating completely replace the body's complement of water in

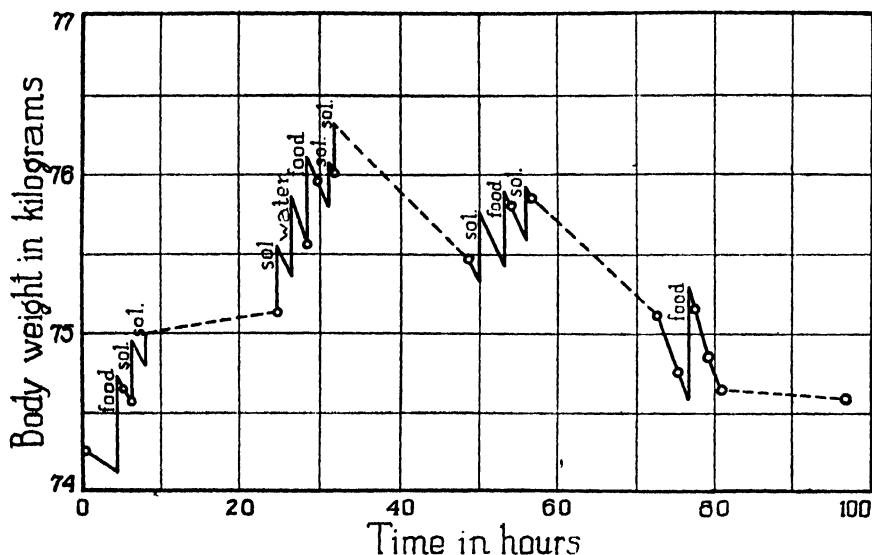


FIG. 10. CHANGES OF WATER BALANCE, INDICATED BY THE BODY WEIGHT, OF A MAN INGESTING A LARGE QUANTITY OF SALT IN ADDITION TO THE REGULAR DIET

The attempt was made to ingest salt water faster than it could be eliminated. Within 50 hours, 52 grams of NaCl and 25 grams of NaHCO_3 were taken, with enough water to form a solution of about three times the osmotic pressure of blood serum. Considerable additional water could be ingested at any time without producing a rapid diuresis, as is shown at the twenty-seventh hour. After the second day no lasting gain of weight was obtained, and the rate of elimination of water was increased.

nificant quantity of water passes along throughout the intestine.

Experiments are readily performed in trying to ingest water faster than it is eliminated as urine (1). Whereas ordinary catabolism furnishes about 40 cc. of urine per hour in an average man, rates of excretion up to 2000 cc. per hour have been reported, and nearly any individual can attain 1000 cc. per hour. It is physically impossible to ingest water at a much greater rate than this for many hours on

about 26 hours. This extreme treatment leaves the body with almost exactly the volume and concentration that it originally had.

On the other hand, it is possible to deny water to the body. Ten per cent or more of the body weight may be lost without unusual symptoms appearing (1). This loss may be completely replaced by drinking water alone, and if drinking continues after repletion, then diuresis occurs to carry away the excess. The precision

with which the original body weight is again reached in such an experiment is astonishing.

How does the body know when its proper water content is present, so that water in excess is not retained, and water short of saturation is tenaciously held? Saturation evidently is related to concentration; and it is legitimate to refer the water to the amounts of salts and the salts to the amounts of certain organic substances such as certain proteins, leaving to one side the problem of how the amount of these in turn is regulated in body or cell. Even the blood regulates its concentration and its volume with such an accuracy that dilution can scarcely be detected during a large diuresis (55). The body responds by distinctly increased water excretion to an ingestion of as little as 100 cc. (2), which gives a decrease of concentration of less than 0.2 per cent if this water becomes distributed equally throughout the body.

Though the body does not retain pure water that is administered in excess of saturation, certain solutions will be retained for longer or shorter periods. An experiment of this sort is shown in figure 10. The mixture of NaCl and NaHCO₃ which is ingested along with less than enough water to make it approximately isotonic with blood, does not lead to a sudden faster elimination of water through a diuresis such as follows water-drinking. There is instead a prolonged slight increase in the rate of urinary water excretion, so that body weight is lost more rapidly than on an ordinary diet. Similar experiments have often been reported (47, 39, 50, 1, 18).

A large number of different solutions may be compared in order to see which salts hold water in the body for the longest time (2, 7). Such experiments are shown in table 3. The salts which do

not give rise to prompt excretion of the water are of two kinds: first, those like sodium chloride, which seem to simulate closely the composition of blood plasma, and second, those like calcium chloride, which are not absorbed to any large extent. Sodium bromide imitates sodium chloride; while sodium iodide and potas-

TABLE 3

Rates of elimination of water by a man after drinking, in each experiment, 1000 cc. containing a salt in a concentration approximately equal to that of the blood plasma

SOLUTE	CONCENTRATION IN PER CENT	CONCENTRATION OSMOLAR	TOTAL CC. EXCESSIVE WATER EXCRETED WITHIN 6 HOURS	MAXIMAL RATE OF WATER EXCRETION, IN CC. PER HOUR
—	0	0	970	790
NaCl	1.0	0.31	190	111
NaBr	1.7	0.30	50	75
"Locke"	0.9	0.28	80	49
NaCl+NaHCO ₃	0.75+0.36	0.31	280	114
NaHCO ₃	1.45	0.31	490	416
NaI	2.6	0.31	670	650
KCl	1.3	0.31	750	460
KCl+NaCl	0.43+0.67	0.31	690	810
KCl+CaCl ₂	0.65+0.85	0.31	340	330
Urea	1.9	0.32	560	673
CaCl ₂	1.7	0.37	70	93
Na ₂ SO ₄	1.8	0.32	50	71
Na ₂ HPO ₄	1.7	0.30	60	75

sium chloride do not. Fluid of a composition similar to blood plasma seems to deceive the regulatory tissues into retaining it over a number of hours or days. But within two or three days the body weight regulates to normal.

It must be obvious that water taken simultaneously with food is also usually

retained. During the periods between meals catabolism is constantly reducing the organic constituents of the body to carbon dioxide, urea, and other substances. As these are formed and excreted, water is also formed and liberated from the tissues, and it likewise is excreted. At the absorption of food, anabolism builds water into the tissues along with glycogen, amino acids, and the like. Since all food which is absorbed is retained by the body without limit, it is natural to ask whether water is retained in proportion to the quantity of food. Experiments show that the proportion between water and food is not a direct one, even for a single food substance. The correlation of the amount of water with foods of different characters is still more complex. And the rôle of salts in conjunction with these foods is at present not at all understood.

Water may be made to stay in the body over shorter or longer periods by the administration of various specific substances. Pituirrin is one of these that has received particular study (55, 7). Its constant presence in the normal body suggests that it plays a major rôle in the normal everyday water-balance. It is supposed by some investigators that the rate of activity of the posterior lobe of the pituitary gland may make the difference between obesity and slenderness. Other endocrine substances affect water-balance either directly, or through the pituitary, or through the liver, or through the circulation (51, 52, 44). Numerous drugs influence water-balance over relatively short periods of time.

DISTRIBUTION OF WATER AMONG TISSUES

The water-balance of the body must be considered also in relation to the individual tissues. Measurements of the water content in plethora and in desiccation have been made in various mammals (32, 64,

43) and in frogs (67, 40), under conditions of plethora and thirst. Undoubtedly the shifts of water among tissues must be analysed in the same way as the shift between organism and environment, before the regulation of water content will be understood.

It must be pointed out, as is indicated in figure 4, that various tissues normally differ from one another in their osmotic pressures or vapor tensions, yet are in perfect fluid equilibrium.

A few kinds of freshly isolated animal and plant tissues have been studied with respect to the exchanges which occur when they are put into media of various concentrations. Thus, slices of potato or of carrot give initial rates of water exchange which are nearly proportional to concentration (65). There is no exchange of fluid in an isosmotic concentration. Mammalian connective tissues (60), frog muscles (42), and skin (15), have been studied in a similar way, with like initial results.

WHAT HOLDS AND REJECTS WATER?

There is no doubt that the water present in tissues is held there in a variety of ways. Some of it depends upon osmotic forces, some upon colloidal forces, some upon chemical forces. It is possible to think of the tissues or cells as sponges, holding water up to a certain saturation level. But it seems less promising to consider each tissue as a block of protein-gel containing various partially diffusible compounds than to consider each tissue as a heterogeneity of membranes. Just as the rate of passage through the skin of the frog is studied in relation to the various forces operating, so the exchange through each tissue structure and cell structure may eventually be measured.

The ultimate problem of the regulation of water balance must recognize not merely the concentrations or proportions of each

constituent and force. For, most organisms, though materials be supplied in the proper relative amounts, do not at all times incorporate them. Rather, regulators of water balance and of any other balance are able somehow, directly or indirectly, to ascertain and control the *absolute* quantities of substance. Were content merely a matter of proportions, all constituents would be lost at the same

relative rates throughout total starvation.

Problems of growth, size, and proportions are inseparable from the problem of water balance. Essentially water balance is independent of biochemical and nutritional factors, for such factors may easily be supplied; there then manifests itself an organism which goes on regulating its own constitution.

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SEX, SPECIES, AND RACE DISCRIMINATION BY MANOILOV'S METHODS

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INTRODUCTION

EVIDENCE purporting to discriminate the sexes and to afford a classification of individual groups of organisms on the basis of physiological and chemical differences has been the subject of many speculative discussions. Speculation on this question is, however, premature, for despite the rather impressive amount of statistical and experimental data that has accumulated since such work was begun, we have as yet no sure way of ascertaining whether the differences involved are of a qualitative, quantitative, or environmental nature. Manoilov attempted to ascertain the nature of the differences involved and presented certain chemical methods the application of which, he believed, could produce characteristic reactions by which male and female blood and tissue extracts as well as the blood and tissue extracts of groups of organisms could be easily differentiated. He attributed these reactions to qualitative differences in the blood.

Before taking up Manoilov's work, it will be advantageous to consider briefly the various views concerning sex differentiation and views concerning differences between groups of organisms. Two theories in regard to the factors involved in these phenomena of sex are prevalent. The first is that difference of sex is predetermined by the presence or absence of a particular chromosome. This contention is supported by genetic evidence.

Second, physiological studies suggest that sex is differentiated either by differences in metabolic level (quantitative differences) or by the elaboration of specific secretions called hormones (qualitative differences). Moore ('25) suggests that these two views are not contradictory but are merely different manifestations of the same physiological condition. Riddle ('14 a and b, '15, '16, '20, '23, and '24), on the basis of his investigations, is of the opinion that sex is not "fixed" but "plastic," and is dependent upon the environmental conditions.

The fact that qualitative chemical differences between groups of organisms do exist is conclusively proved by the work on sero-diagnosis (Mez and Ziegenspek, '26) as well as by that on the chemical constituents of respiratory pigments. From serological studies we learn that organisms may be divided into groups on the basis of agglutinating reactions of the blood. It has been assumed that these different reactions are produced by specific substances the chemical nature of which is unknown. Landsteiner's ('00) studies on human blood have shown that there are four blood groups in the species and that they have a wide geographic distribution.

Again we find that organisms fall naturally into groups on the basis of differences in the crystal structure of their respiratory pigments. Reichert and Brown's ('09) extensive studies on the crystallography of the haemoglobins indicate that these substances exist in a great number of modifications "each modifica-

tion being characteristic of the form of protoplasm, the organ, the individual, the sex, the species, and the genus." On the basis of these modifications, as evidenced by differences in crystal structure, the groups (genera, species, sexes, etc.) may be easily differentiated. These are probably diversities in chemical constitution based on stereo-isomerism, but the work of Willstätter and Stoll ('13) on chlorophylls indicates that at least in this group specific differences in chemical composition also exist. Some indication of similar differences in the haemoglobin may be seen in Helff's ('27) work on the different rates of oxygen consumption in the larvae of various species of *Amblystoma*. It is very probable that this differential rate of oxidation is correlated with specific chemical characteristics of the respiratory pigment.

DISCRIMINATION OF SEXES

Manoilov had long been interested from the standpoint of forensic medicine in the problem of the determination of sex by means of blood reactions, but it was not until 1920 that he first succeeded in discriminating male and female blood, even in a small percentage of the cases. In the two years which followed, he devoted his time exclusively to this problem; working by the method of trial and error, changing and modifying his technique until he had arrived at a method which gave a much higher percentage of correct results than any other. From the thirty-six modifications used, he picks three which he says give the best results. Of these the "Third Modification" is the one which is now used almost exclusively by Manoilov as well as by other investigators. The method is as follows (Manoilov, '23 a):

To 3 cc. of unwarmed erythrocyte emulsion the following reagents are added in the order given:

1. 1 per cent aqu. solution of papayotin Merck (filtered) 10 drops.

2. 1 per cent alcoholic solution of dahlia (Grübler) or methyl violet (filtered) 3 drops.

3. 1 per cent aqu. solution potassium permanganate 10 drops.

4. 1 per cent hydrochloric acid (40 cc. conc. hydrochloric acid plus 60 cc. water) 3 drops.

5. 2 per cent thiosinamine solution 5 drops.

Manoilov placed special emphasis upon the addition of the reagents in the proper order. Moreover, the solution must be allowed to stand 1-2 minutes after the addition of the first reagent, it must be stirred but not shaken after the addition of each of the first three reagents and be shaken after the addition of the fourth. If all these precautions have been properly observed a solution containing male blood should be colorless, while one containing female blood should show a violet tint.

In preparing the blood emulsion Manoilov added 4-5 volumes of physiological salt solution to 1 volume of blood and stirred this until a semi-transparent (*halbdurchsichtige*) emulsion was obtained. Emulsions of greater or less concentration may also be used, but it is necessary in such cases to alter in a corresponding way the number of drops of the reagents added. That is, the dye and the other reagents must be standardized with respect to the emulsion used. Thus, if a certain emulsion shows no color either with male or female blood, it is necessary to decrease the number of drops of hydrochloric acid added until the male blood alone becomes colorless while the female remains partly colored. Decreasing the amount of the fifth reagent will also accomplish this purpose. If, on the other hand, the emulsions from both sexes give a color, then the amount of dye added must be decreased until a differentiation is obtained.

Using this method Manoilov declares that he obtained positive results in 86-96 per cent of the 530 cases investigated. In many instances, however, he obtained

"reversals," male emulsions gave female reactions and vice versa. In these the investigator introduced a "correction." If a male emulsion gave a female reaction he added 10-20 drops more of potassium permanganate, 2 drops of hydrochloric acid and sometimes 3 drops of thiosinamine. After these additions and after shaking, the fluid usually lost its color. In case of female emulsions which gave the male reaction, more of the third reagent was added; whereupon a darker color was obtained. As a control the same number of drops of the reagent were added to a typically colorless male emulsion and shaken; the emulsion remained colorless, or became slightly darker. By this means Manoilov was able to greatly increase the percentage of correct results obtained. However, if we grant the validity of such a procedure, which is at best questionable, it is evident that it could not be used in cases in which the sex is unknown, for in such instances we could have no means of recognising a "reversal" as such. For this reason the "correction" procedure has very little practical value.

This first work related entirely to the determination of the sexes in animals, but it was not long before Manoilov ('23 b) extended his work to a consideration of the same problem in plants. In view of the close chemical relationship which has been demonstrated by Nencki, Marchlewski and Zaleski (see Reichert and Brown, '09) to exist between chlorophyll and haemoglobin, it seemed not at all improbable that they would show similar chemical relations in this case. Manoilov investigated dioecious plants by extracting the green leaves with 60 per cent alcohol for 1-2 hours at room temperature. The reagents of the third modification were added to 3 cc. of such extracts and in all cases correct results were obtained.

The publication of these results at-

tracted wide interest and the question of the chemistry of the reaction involved and the rôle of the various reagents quickly came to the fore. Manoilov himself said little on this subject in his first two papers ('23 a and b), but in his third article ('24) he sets forth his ideas on these points and gives the results of some experiments undertaken in order to determine which reagents play the most important part in the reaction. For this purpose he made a number of tests with male and female blood, adding the reagents in the proper order but omitting one or the other of them. In this way he found that the omission of any of the five reagents prevented the reactions from occurring and no discrimination was obtained. (These results, it may be remarked, do not accord with those of later investigations.) From the consideration of experiments of this nature, Manoilov recognised that an oxidation process occurs in the reaction and he assumed that the papayotin and thiosinamine have the most important rôle to play; the dahlia, potassium permanganate, and hydrochloric acid merely exerting an oxidation effect. ("Aus der Tabelle ist ersichtlich, dass bei der Reaktion ohne Zweifel ein Oxydationsprozess vor sich geht. Ausserdem ist deutlich zu erkennen, dass Papayotin und Thiosinamin die wichtigste Rolle spielen. Die Reagense N.N. II, III und IV beteiligen sich und üben bei der Reaktion eine Oxydationswirkung aus.") The basis of the reaction, he thinks, rests upon a qualitative difference between the bloods of the two sexes, a difference which is due to the presence of male and female sex hormones which produce certain slight changes in the blood that are discoverable by this procedure.

DISCRIMINATION OF RACES

Manoilov in 1925 presented a series of empirical methods by means of which

certain nationalities could be discriminated chemically. In view of the fact that serological studies have shown that there are specific chemical differences between groups of individuals, a specific substance, analogous to the sex hormones differentiating the sexes, was supposed by the author to be responsible for these differences. To quote, "Auf Grund der Tatsache, dass die Geschlechtsbestimmungsreaktion durch Blut die Unterscheidung der Geschlechter voneinander ermöglicht, war es für mich klar, dass bei Vorhandensein von Hormonen für die beiden Geschlechter- ganz analog auch im Körper spezifische Rassensubstanzen ausgescheiden werden müssen, die den verschiedenen Rassen einen ganz spezifischen Charakter verleihen." He thought that these methods gave an index to the chemical properties of the unknown specific substances characterizing races and nationalities. These methods were of the same general nature as those that were used for the discrimination of sexes. According to this author, however, the question of sex plays no important part as far as these methods are concerned.

The following is the method used to discriminate Russian from Jewish blood (Manoilov, '27):

For these reactions the following reagents are needed:

1st reagent—1 per cent solution of methyl blue (Grübler).

2nd reagent—1 per cent alcoholic solution of cresyl violet (Grübler).

3rd reagent— $\frac{1}{4}$ of 1 per cent solution of silver nitrate.

4th reagent—40 per cent solution of hydrochloric acid.

5th reagent—1 per cent aqueous solution of potassium permanganate (freshly prepared).

The reaction proceeds in the following way: Add to 3 cc. of the unheated emulsion of red blood corpuscles (3-5 per cent) or directly to the coagulum of blood three to four times that much (in volume) sodium chloride (physiological solution) and mix

with a glass stick so as to obtain a rather thick emulsion. Then add 1 drop of the first reagent, shake; 5 drops of the second reagent, shake again; 3 drops of third reagent, shake; 1 drop of fourth reagent, and lastly 3 to 5 drops of the fifth reagent. The result will be correct if the fluid with Jewish blood proves to be paler than that with Russian blood. In the Jewish blood the cresyl-violet must disappear entirely or almost so, and the blue or blue-green shade alone remain; in Russian blood the cresyl-violet will partly remain insoluble, and we see generally a blue-red coloring.

The blood was obtained only from individuals whose hereditary history had been investigated, i.e., those that had had three or four paternal as well as maternal ancestors of the same nationality. It was upon these results that the conclusions were based. When this method was applied to Russian and Jewish blood the resulting fluid was a paler shade of green with the Jewish blood than with the Russian blood. Manoilov explains this phenomenon by saying that the "cresyl-violet dissolves in the Jewish blood, whereas in the Russian blood it dissolves only partly but never completely." To get good color difference the author suggests modifications of the amount of reagents added.

No clear cut notion can be obtained from this work concerning the nature of the chemical reactions involved or the functions of the various reagents used. The impression is conveyed that by incorporation of the various ingredients prescribed, in the manner of a cook book recipe, in which so much of this and so much of that is added, some kind of result is obtained, sometimes good and sometimes bad. Cresyl-violet disappeared because it became oxidised. Oxidation, it was supposed, took place only in the presence of finely divided silver chloride, which is formed as the result of the reaction, and substances (no mention is made of their nature) can by this means be

eliminated from the field of action by adsorption. That chemical discrimination between nationalities rests upon varying degrees of oxidation seems to be the predominating idea.

From these results it was concluded that oxidising processes go on more readily in Jewish blood than in Russian. This method has been found accurate according to Manoilov in 91.7 per cent of the cases tested, that is, when pure Russian and pure Jewish blood are tested. The blood of other nationalities: Chinese, German, Estonian, Finnish, Polish and Armenian, was likewise studied, but owing to the lack of material no definite conclusions were drawn concerning the results. However, these other nationalities, Manoilov, says, could be readily discriminated from one another by this means.

The blood of children born as the result of mixed marriages was also studied. The blood of the offspring from a pure Russian father and a pure Jewish mother gives a resulting color that is stronger than the color obtained from the Russian. Again if the father was pure Russian and the mother (pure?) German, the result differs from the purely Russian. From this evidence it was concluded that there were indications of the influence of one nationality upon another. In one case the paternity of a disputed child was determined by the use of this method.

DISCRIMINATION OF SPECIES

Since Manoilov considered that he had succeeded in discriminating nationalities, he next turned his attention to the chemical differentiation of species (Manoilov, '27 b). Working upon the basis that the physico-chemical condition of the blood is the key to the solution of the problem of the origin of species, a series of chemical procedures was presented. These were

modifications of the one used for the chemical differentiation of nationalities. With these modifications a correct answer in 100 per cent of the cases investigated was obtained, according to Manoilov, when cattle and horse sera were used. Sera of pigs, dogs and man were likewise used. However, no detailed tables of results were published. It was hoped by this investigator that by using blood of cattle and horses, where large quantities of blood are available, the reaction between the serum and the reagents in the procedures in question might be understood. These methods were derived likewise upon an empirical basis. As in the method for the discrimination of races, sex appears to have no importance.

The following method was used and recommended by Manoilov. It is called the "First Modification" and is quoted from his paper:

1. Reagent Brenzkatechin, 2 per cent of aqueous solution.
2. Reagent Methyl blue, 0.1 to 0.2 per cent aqueous solution.
3. Reagent China blue, 0.5 per cent aqueous solution.

The reaction must be performed as follows: Take test tubes as sterile as possible or at least irreproachably clean, into which pour 3 to 5 cc. of unheated serum; then add five drops of the first reactive-Brenzkatechin; shake; add next one drop of second reagent, methyl blue, shake thoroughly once more; finally add 1, 2, or 3 drops of the third reagent, china blue, and shake violently.

After the addition of the above named reagents, the serum of horses turns green to greenish, while the serum of cattle turns from blue to dark blue. To facilitate the color difference normal saline solution is added. There were three other modifications, using different dyes which gave similar results. China blue was, however, used in all of the modifications.

At first fresh serum was used; later it was found that the same result was ob-

tainable with old serum, the only difference being that of intensity of color. From this it was concluded that the reaction was chemical rather than biological. Since a correct result is obtained with coagulated serum the conclusion was reached that the unknown substance is not an enzyme but is an albumin complex; there being a characteristic one for each species.

The functions of the respective reagents and the nature of the reactions involved in these procedures is likewise not understood. A biacid salt of methyl blue is postulated. Brenzkatechin (O-dioxybenzol) was chosen because it was very susceptible to oxidation. China blue is added as an intensifier: it has no effect upon the resulting color of the horse serum but intensifies the shade of color when cattle serum is used.

A REVIEW OF THE WORK OF OTHER INVESTIGATORS

The results which have been reviewed have attracted the attention of many investigators, for it was seen that if the method could do all that was claimed for it, it would be of the utmost importance in many different fields. A number of workers set out to repeat Manoilov's work and to determine the limits of applicability of his method by means of experimentation upon extracts from various plants and animals. Much of this work gave confirmatory results but from the very start a large number of failures was recorded; some could no doubt be attributed to inexperience, but others seemed to justify the conclusion that the procedure was not applicable to these cases.

Calisto ('26) experimented with guinea pigs and found that this method of sex discrimination failed entirely; males gave the reaction of females as often as they

did that for males and vice versa. He therefore concluded that the reaction could not be applied for the differentiation of sexes in guinea pigs.

Banta and Satina ('25), on the other hand, obtained positive results with *Cladocera* and found that parthenogenetic females gave a result intermediate between that of normal males and normal females.

Satina and Blakeslee ('26a) followed up this work by a study of plus and minus mucors in which positive results were obtained in about 95 per cent of the cases. The same investigators ('26 b) applied Manoilov's method to tissue extracts of the green leaves of dioecious plants and again obtained positive results but found differences between old and young leaves and between tissues extracted for varying lengths of time. In view of the fact that in Satina and Blakeslee's experiments with plus and minus mucors a definite biochemical difference was established on the basis of the catalase content, the foregoing results seemed to indicate that the Manoilov reaction was of a quantitative rather than of a qualitative nature, and it therefore seemed imperative that an exact study be made of the chemical nature of the method.

The first thorough analytical investigation of the mechanism of the reaction was made by Alsterberg and Håkansson ('26) and was confirmed in the main by the work of Galwialo, Wladimirow, Winoogradow, and Oppel ('26), carried out independently at about the same time. Alsterberg and Håkansson tested a great number of different sorts of extracts of both animal and vegetable origin according to Manoilov's method and found first of all, that the test was noticeably affected by the dilution of the extract; as the concentration of the extract was decreased the final color of the test became weaker. This would indicate that there is some

substance in the blood which, if present in large amount, causes a darkened color of the test; if it is present only in small amounts a lighter color is obtained. Since the reaction is undoubtedly an oxidation-reduction process they concluded that the substance involved is probably a reducing agent. The result of the test would then depend upon whether the oxidising agent or the reducing agent is present in excess. In order to demonstrate that this view is correct, the investigators made some experiments, using instead of blood or plant extracts, a number of different reducing agents such as sodium bisulphite, sodium nitrite, oxalic acid, etc., adding the reagents of the Manoilov procedure to solutions of these substances of varying concentrations. In this way a whole scale of different colors was obtained according to the concentration of reducing agent used. This point is illustrated in the following table taken from their paper:

Natriumbisulfit, 2 proz. wässrige Lösung; zur Probe wurde (nebst 3 ccm Aqua dest.) die unten angegebene Anzahl Tropfen hinzugesetzt. Im übrigen erfolgte die Ausführung der Probe nach *Manoiloffs* Vorschrift.

DISULFIT ANZAHL TROPFEN	FARBE DER PROBE
1	farblos
2	farblos
3	farblos
4	rosa
5	ziemlich stark violett
6	sehr stark violett
7	noch stärker violett

This would indicate that the Manoilov reaction depends not upon the presence of any specific substance like a sex hormone, but rather upon the relative amount of organic substance present in the extract.

These investigators then proceeded to study the various reagents used in the method with respect to their function and specificity. They found that the papayo-

tin, far from playing the important rôle that Manoilov had assigned to it, could be replaced by a number of purely inorganic reducing reagents like sodium bisulphite and could even be omitted without seriously affecting the result. They concluded that it simply served the purpose of making up a sufficient quantity of reducing agents necessary for the test. As for the dye (dahlia) its main function is probably that of an indicator. The permanganate serves as an oxidising agent which, by its reaction with the dahlia, gives an indication of the amount of reducing substances present. If there is an excess of reducing substances, a part of the potassium permanganate will go to oxidising them; as a result there will not be sufficient oxidising agent to completely decolorise the dye; thus a colored solution (female reaction) will be obtained. On the other hand if there is an excess of oxidising substances present the dye will be completely oxidised and the male reaction (colorless) will result. This occurs most readily in an acid medium which is supplied by the hydrochloric acid. The fifth reagent, thiosinamine, is another reducing agent, which by its addition after the foregoing reaction has occurred, serves to reduce the excess of permanganate and the manganic oxide to colorless compounds so that the color of the solution is more easily seen. On the basis of these results the authors are led to conclude that the reaction depends upon a quantitative rather than a qualitative difference between the sexes. If this is so it indicates that, in general, reduction processes prevail in female organisms while oxidation processes prevail in male ones. Alsterberg and Håkansson, however, deny that the method has such universal applicability as has been claimed for it, pointing to the fact that failures and reversals are often obtained, for the

reason that the amount of reducing substances present in the same organ may change considerably even in a short time. In other words they believe that the greater or smaller amount of reducing substances present is not at all specific for the sexes and since this is really what the Manoilov test measures, its accuracy cannot be confirmed.

The work of Galwialo, Wladimirow, Winogradow and Oppel ('26) was undertaken with the same object as that of Alsterberg and Håkansson and was pursued along much the same lines. They carried out a number of experiments in order to determine the part which the various reagents have to play in the reactions involved and according to them the mechanism of the reaction is explained in the following way: The permanganate oxidises the dye in acid medium, whereupon the latter loses its color. In the presence of substances which are more easily oxidised than the dye, however, the amount of permanganate does not suffice and the fluid under investigation remains colored. The thiosinamine serves for reduction of the manganic oxide which is formed. Papayotin is not necessary for the reaction. These results accord perfectly with those of Alsterberg and Håkansson. Galwialo and his co-workers now proceeded to an investigation of the specificity of the reaction. They tested a number of substances with respect to the ease with which they could be oxidised by potassium permanganate and found that the proteins take the first rank in this regard, especially the tyrosine, tryptophane and pyrrol derivatives. All of these are able to reduce large amounts of permanganate, but the reactions with tyrosine and tryptophane become negligibly small under the conditions of the Manoilov reaction (acid medium). Therefore these authors are led to believe

that the reaction depends mainly upon the relative amounts of pyrrol derivatives present in the substance under investigation. The test is not specific, however, for many other organic compounds are able to reduce potassium permanganate under the conditions of the Manoilov reaction, although to a much slighter degree. This work, the authors believe, throws some doubt upon the investigations of the workers who have assumed a specificity of the reaction but have not taken into account the protein content of the fluids investigated.

Schmidt and Perewoskaja ('26) came to much the same conclusion on quite different grounds. They found that female blood serum has a higher specific gravity than that of male serum, owing to the fact that female serum contains an average of 8.5 per cent more proteins than does the male. The Manoilov reaction then, according to their view, merely furnishes an indication of the relative amounts of protein present. It is obvious that, upon this hypothesis, the "reversals" so frequently obtained are readily explainable, for it would only be necessary that a male serum have an abnormally high protein content in order to give a reaction indicating that it belonged to a female or that a female serum have an abnormally low protein content to give a male reaction.

This explanation is borne out by the work of some other investigators. Riddle and Reinhart ('27), working with pigeons and ring doves, found frequent reversals when examining blood samples from reproducing individuals; thus indicating that at that time the blood of the male contained more organic substances and the blood of the female contained less organic substances than normally. Riddle, in earlier studies, had shown that during the reproductive period there is an in-

crease in metabolism in the female and that it is probable that there is a corresponding decrease in the male. He therefore concludes, that the amount of organic substance in the blood varies with the metabolic rate and that the Manoilov reaction constitutes a test for metabolic level, which can be used as a sex test only at those periods when the metabolic rate is fairly constant. This hypothesis may explain the failure which Calisto encountered with guinea pigs, since he took no account of the oestrous period, state of sexual excitement or other factors which might have influenced the metabolic level of his individuals. Further experiments on these animals, with due consideration of the factors listed above, may go far toward explaining Calisto's results and substantiating Riddle's conclusions.

Falk and Lorberblatt ('27) experimented with the Manoilov method for the discrimination of the sexes and found that dahlia could be replaced by pararosaniline, the simplest representative of the triphenylmethane series of dyes, and that the papayotin could be replaced by proteins such as albumin. It must be noted, however, that such compounds must invariably be present. The thiosinamine may be replaced by various reducing substances such as sodium thiosulphate, ferrous sulphate, oxalic acid, hydrogen peroxide, so that its function must be to effect the reduction of the excess potassium permanganate. These investigators also found that a variation of the concentration of the original extracts does not influence the result if the concentration of the oxidising agent is suitably adjusted. This work was carried out with standard ovarian and orchic extracts and indicates that the reaction involved in the Manoilov method is essentially an oxidation reaction, although the exact part played by the ovarian and orchic substances and by

the various materials from other sources in analogous tests is uncertain.

Poliakowa ('27), made use of the Manoilov method for race determination. The blood was obtained from ninety-nine individuals of mixed and pure marriages. In some instances blood was taken from father, mother and child. When the father and mother were of the same nationality it was called a "pure marriage" and when the father and mother were of diverse nationalities it was called a "mixed marriage." Before carrying on the work, Poliakowa first determined the resulting color of the reaction with the bloods of different nationalities. It was found that each nationality had a characteristic color. The following is a table giving the shade of color for the different nationalities (table 1):

Russian.....	reddish
Jews.....	blue-greenish
Esthonians.....	reddish-brownish
Letts.....	reddish-brownish
Koreans.....	reddish-violet
Polcs.....	reddish-greenish
Kirgis.....	bluish-greenish

On the basis of these shades the results were classified.

This work was only of a preliminary nature since very few individuals of any particular nationality were studied. The results of this investigation corroborate the findings obtained by Manoilov. If the blood is that of a child born of parents of a racially pure marriage (father and mother of the same race), the blood will give the same reaction to the reagents as the father's and mother's only the shade will be slightly paler. The following table (table 3 taken from Poliakowa's paper) summarizes the results of the effect of one nationality upon another:

Russians X Germans.....	child Russian
Russians X Polcs.....	child Russian
Russian X Finns.....	child Russian

Jews × Russians.....	child Jew
Jews × Esthonians.....	child Jew
Esthonians × Poles.....	child Esthonian
Letts × Germans.....	child Lett

Poliakowa considers the Manoilov method as of great practical importance, since the parentage of a child may be determined on the basis of the two following conclusions:

1. If the child's and mother's blood give a different reaction, the father does not belong to the mother's nationality.
2. If the child has a distinct race reaction which does not correspond to the mother's nationality, the father may belong to the nationality the reaction of which has been found in the child.

These results, however, are of value only in racially pure marriages.

SUMMARY

Manoilov simply by modifying various mixtures of reagents has discovered methods by means of which races, sexes and species can be differentiated chemically, according to his assertion. Although these methods convey the impression of being taken out of a cook book, nevertheless the fact remains that under certain conditions

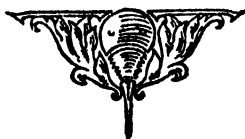
correct results may apparently be obtained. Indeed, it is Manoilov's contention that in a short time he will have a series of methods whereby all groups of animals, human beings included, can be differentiated from one another. Has he discovered a delicate test for the physico-chemical differentiation between sexes, races and species? With regard to the method for the differentiation of sexes, it has been shown that it is to a certain extent a measure of organic material present; a test involving an extremely variable factor. That different species may possess different rates of oxidation has been shown by Helff for *Amblystoma*. It may be that Manoilov detects the different rates of oxidation in different races and species by the use of his methods. But if the difference is a question of rates of oxidation and the rates of oxidation are correlated with metabolism, then by simply modifying the metabolic level one could obtain at one time a test indicating a male, at another time one indicating a female; or at one time a test indicating a monkey, at another a human being.

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THE BIOLOGY OF HOOKWORMS IN THEIR HOSTS

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INTRODUCTION

DURING the last quarter of a century a great deal of attention has been given to the group of parasites known as the hookworms, which infest man and certain animals. The chief reason for this attention has been the importance of these parasites in the field of public health, but out of the work have come many observations which are of interest from a purely biological point of view. Although these contributions have dealt with both the free living and the parasitic stages, it is with the latter that this paper will primarily be concerned. The chief purpose is to summarize certain experimental studies on the biology of the species of hookworms parasitic in cats and dogs. Although an attempt will be made to mention representative papers from the literature of this field, emphasis will be laid on the work of a particular group done under the general direction of Dr. W. W. Cort and supported by a grant from the International Health Division of the Rockefeller Foundation. These species found in cats and dogs furnish the most convenient material for experimental work. Although these forms are related closely to those found in man, conclusions from the experiments should be applied to the human hookworm only with the greatest caution.

SPECIFICITY OF HOOKWORMS

It will be necessary first to outline briefly the relation of the hookworms of

dogs and cats to those of man and to other similar parasites of animals. As a group the hookworms are relatively specific parasites, that is, a particular species is usually found in only one species of host. There are, however, a few which are common in more than one host and most species have been found occasionally in hosts more or less closely related to their normal hosts. In addition to these recognized species differing morphologically, there are certain strains which, although identical morphologically, differ physiologically in their specificity to particular hosts.

To many the forms occurring in man are of greatest interest. The problem as to where man acquired these parasites is still unsolved. It has been suggested that he acquired them from two sources (Cameron, 1927 c). In the first place there is the possibility of acquisition of one species, *Ancylostoma duodenale*, from the carnivores. Although entirely distinct from the species now commonly found in carnivores, this human species is occasionally recorded from various members of the cat and dog families. Various species of this genus such as *A. caninum* and *A. braziliense*, common to members of these families, are found occasionally in man. On account of these facts it has been suggested that man acquired this parasite by his association with carnivorous animals in early human and not in prehuman days.

In the second place, man may have acquired certain parasites hereditarily. That is, they or their progenitors may

have inhabited the ancestor of man in prehuman days. Such a possibility has been suggested for the other hookworm of man, *Necator americanus*. Other species of this genus are found, not in animals with which man has been associated since arriving at the human level, but in primates related to the hypothesized ancestors of man. Nor is this human species found as an occasional parasite in carnivores, but the records from animals other than man are from the primates and herbivores. Furthermore, this species is less pathogenic to man than the former, and on this basis is considered by many to have been associated with man for a longer time, dating probably from prehuman days.

Of the forms occurring in animals but related to those of man, two species have been dealt with primarily in the experimental work mentioned above. The first, *Ancylostoma caninum*, is the common hookworm of dogs in the United States and many other parts of the world. It is also frequently found in cats, but as will be explained later the forms from this host are probably a physiological strain or incipient species. This species has also been reported as an occasional parasite of various members of the families *Canidae* and *Felidae* and of a few other animals. There are, moreover, a very few records of its occurrence in man. The second form, *Ancylostoma braziliense*, with which *A. ceylanicum* is now considered synonymous, is commonly found in both cats and dogs in certain localized regions scattered over the whole world, but no strain differences have yet been demonstrated. This parasite has also been reported occasionally from other *Canidae* and *Felidae* and has been found in man on several occasions, but usually in small numbers (Sarles, 1929 a). Other species of this genus are found in a variety of animals, mostly of carnivorous habit.

There are also species in various animals which are related to the *Necator* of man. Two species of this genus are reported from other primates and one from the domestic pig. There is some discussion as to whether this latter species, *Necator suillus*, is distinct from the human species, but it certainly seems to be different in regard to its specificity at least. Among the other genera of the same family is one species, *Uncinaria stenocephala*, which we should mention because it is the common dog hookworm of Europe and is common in foxes in America. It has also been used frequently for experimental work.

Before we enter into a discussion of the experimental work on these parasites it may be well to review the chief points in their life cycle. The eggs are passed in the feces of the host, and develop in the soil when subjected to proper conditions of temperature, moisture and soil texture. The larvae, which hatch in a few days, are infective in a week or so and seek the upper surface of the soil when there is sufficient moisture for them to exist there. Whenever they are brought in contact for a few minutes with the skin of the host, they burrow into the intact skin until they reach a blood vessel. They are then carried passively to the heart and lungs. When stopped in the capillaries of the lungs they work their way into the air passages, up the trachea to the mouth, are swallowed and carried to the intestine, where they mature. Experimentally, infestation can also be produced by ingestion of the infective larvae and this may occur in nature, especially with certain species. In the growth process in the intestine they undergo two moults. At the first of these they acquire a so-called primitive mouth capsule and at the second a definitive mouth capsule. With the aid of these and the teeth which they contain, the growing worms attach themselves to the mucosa, and live at the expense of the

host on blood and tissue. At maturity copulation occurs and the females lay enormous numbers of eggs into the lumen of the intestine over a long period of time.

ENTRANCE INTO THE HOST

The first point for us to consider in the biology of the host stages of the hookworm is obviously the entrance into the host. Skin penetration, which Looss (1911) discovered and described in detail, is probably the most common method of entrance, especially into man. Prenatal infection has been recorded as a result of larvae penetrating the fetus in the uterus after skin infection of the mother. Mouth infection may occur in any host, but probably is not common except in such a case as that of a dog eating food which has been dragged on the ground. Mouth infection has frequently been used in experimental work since the actual number of larvae entering can be determined more readily. The practice in our laboratory has been to administer the larvae in gelatin capsules so that there will be no possibility of penetration until the stomach is reached. The possibility of loss in the skin and the lungs is also eliminated by this method. Sarles (1929 d) found only about nine per cent. of the larvae given by skin developing in the intestine of pups as compared to 50 per cent. of a parallel series given by mouth.

Although there seem to be greater hazards for the larvae after they have entered the body by way of the skin, this method of entry is frequently more accessible. In such a host as man, where ingestion of contaminated food is not common, an adaptation for skin penetration is of great advantage to the larvae. Because of this adaptation there has been considerable study made of the reactions of the larvae and certain definite tropisms have been demonstrated (Brumpt, 1921;

Fülleborn, 1924). It appears that the larvae react positively to heat and possibly have a histotropism which attracts them towards the body tissues. For the actual penetration the larvae need among other things something against which they can push in entering the skin. Mud caked onto the skin fulfills the requirements almost perfectly. Water drying on the skin provides a surface film which gives the proper support. The thickness of the skin probably has an effect on the ease of penetration, as does also the condition of the skin in respect to its being softened by water. It has been found, for example, that experimental penetration can be effected much more easily after the skin has been thoroughly scrubbed and exposed to a steam bath. It is apparent, however, that in nature the larvae frequently find the necessary conditions fulfilled.

Penetration of the skin calls forth certain reactions on the part of the host. A variation in the skin reaction of hosts of different ages has recently been demonstrated by the use of *A. caninum* in dogs. Sarles (1929 d) found that young dogs showed not more than a transitory inflammation after the penetration of large numbers of larvae. In old dogs, however, a marked swelling and inflammation began almost immediately and continued for a week or more with pronounced exudation and necrosis at the center of the lesion. The significance of this correlation with the age of the host will be discussed at a later place. Experimental infections of the human skin with practically sterile larvae of the species normal in man produce itching papules which subside after a few days. Typical "ground itch" as seen under conditions of natural infection is usually an open sore complicated by scratching and the action of secondary bacterial infection. An interesting variation in the skin reaction, or more prob-

ably variation in the behavior of the larvae, is the phenomenon known as creeping eruption. Recent work (Kirby-Smith, White and Dove, 1926, 1928; White and Dove, 1928) has shown that these linear advancing lesions of the human skin are due to the penetration of larvae of *Ancylostoma braziliense*, a hookworm fairly common in dogs and cats in certain localities, and occasional in man. Why these larvae migrate just under the human skin and do not migrate under the skin of dogs, cats, monkeys and other animals has not been determined. The larvae of another dog hookworm, *Uncinaria stenocephala*, have also been shown to produce a similar condition (Fülleborn, 1928). The larvae of *Ancylostoma caninum*, however, do not produce these lesions in the human skin, but only papules similar to those produced by the human species (White and Dove, 1929).

MIGRATION TO SEAT OF INFESTATION

When the larvae have entered the body by any route they are still faced with the problem of proceeding to the final seat of infestation, namely the small intestine. After skin penetration a continuation of the boring reactions by which they enter eventually carries them to a blood vessel. Regardless of whether there is a definite reaction for entering the blood stream as has been suggested (see Looss, 1911) or whether it is a random matter, the majority of the organisms do eventually get into the blood stream, and are apparently carried passively to the lungs. When stopped in the fine pulmonary capillaries the larvae penetrate the walls and get into the air spaces. This may be due to their random penetrative movements, or they may by this time have developed a reaction specific for this purpose. In a passage through the bronchi and the trachea Looss found that there was a difference between

the behavior in the dog of the larvae of the dog hookworm, *A. caninum*, and that of the human form, *A. duodenale*. He states that the larvae of the dog hookworm migrated along the surface of the mucous membrane, while those of the human species frequently penetrated the wall of the trachea. He attributes this reaction of the latter to the fact that they were in the unsuitable environment of an abnormal host, while those normal to this host were beginning to develop new reactions suitable for their parasitic existence. The fact that these larvae in the normal host started to grow at this stage will be discussed later. The passage of any considerable number through the larynx is frequently attended by a slight cough in both the animal and human host. Once in the mouth further passage to the intestine is probably purely mechanical and independent of any effort on the part of the larvae.

When the larvae are introduced by mouth and carried to the stomach it seems logical to expect development to begin immediately. The idea has been advanced, however, that the reaction for penetration causes the larvae to enter the walls of the alimentary tract and thus pass through the portal circulation to the liver, then to the heart and lungs as after skin penetration. Other nematodes such as *Ascaris* and *Strongyloides* follow this course, and it has been assumed to be true by Fülleborn (1923) and strongly upheld by Miyagawa and his associates (Miyagawa, 1913, 1916; Shirai, 1926). Yokogawa (1926), however, after a series of experiments with *A. caninum* in dogs, stated that such migration does not occur, but that development begins directly. Fülleborn (1926) confirmed this for another hookworm normal to dogs, *Uncinaria stenocephala*. The writer (Scott, 1928), working with the same form as

Yokogawa but using quite a different technique, has also found that migration does not occur regularly in dogs after oral infection, but that development continues directly.

At the same time Yokogawa introduced another phase of the problem. On the basis of experiments with the human species, *A. duodenale*, in dogs, and the dog species, *A. caninum*, in rabbits, guinea pigs and mice, he concluded that in the abnormal host this migration after oral infection does occur, although it does not occur in the normal host. In the series of experiments mentioned above (Scott, 1928) the writer used for the removal of larvae from the various organs of the host the Baermann isolation apparatus, which had previously been used for the isolation of larvae from the soil. By this method greater numbers of larvae of *A. caninum* were recovered from the liver and lungs of rats than from those organs of dogs. Cats, as will be explained later, may be considered practically an abnormal host for the strain used here. In them very few larvae were found in the lungs and liver. When, however, rats were given very large numbers of larvae by mouth a large proportion were recovered from the lungs, and this was attended by the presence of a severe and often fatal pneumonia. It has not been possible to determine whether the large numbers of larvae given were able to break some sort of resistance of the host and cause a greater migration, or whether only the usual proportion migrated but the numbers were sufficient to produce a pneumonia which prevented the completion of migration and caused an accumulation of larvae in the lungs. It seems clear then that although migration does not regularly occur after oral infection in the normal host, there are conditions under which migration does occur in certain abnormal hosts. Whether

this is correlated with or dependent upon the abnormality of the host, as Yokogawa believes, does not yet seem to the writer to be clearly demonstrated.

THE GROWTH OF HOOKWORMS

One of the most interesting features of a study of the growth of these parasites concerns the point at which growth beyond the infective larval stage begins. It is at this point that development in a partially or completely insusceptible host seems to be inhibited. This raises the question as to whether growth even starts in a host in which it is never completed. Most of the experiments with these insusceptible or abnormal hosts have dealt with rodents of one species or another. Hung (1925) found what seemed to be an increase in the length of larvae passed alive in the feces of rats three days after skin infection with larvae from a mixed culture of the two human parasites. The writer attempted to repeat this with a more extensive series of experiments, using oral infections of *A. caninum*. The data, which have not been published, showed great variation from case to case so that no valid conclusions could be drawn, but the tendency was toward a decrease rather than an increase in length. About the only explanation for this change, if it were a valid one, would be that of a selection, the larger individuals having remained in the host. Measurements of larvae taken from the same animals indicate that an increase in size may have occurred in the host, but the variation from rat to rat was so great that it has not been possible to prove this to be significant. Fülleborn (1927) also found some increase in the size of the larvae of *U. stenocephala* in various rodents, but he also apparently was not satisfied that it was a significant one.

In a host where development is possible

we have a similar problem of determining when and where it begins. Looss (1911) found that in the dog development of *A. duodenale* did not begin as soon as that of *A. caninum*, although the former would develop to a certain extent in very young dogs. He reported that the first appearance of the mouth capsule of the final larval stage comes when the larvae of the dog species are in the upper half of the trachea of the dog, but he has never seen it in the lower half. The moult into this final larval stage did not occur until the intestine had been reached. Examination of many larvae from a number of cases in our series has not revealed this change taking place at this time. But Looss did not say in what proportion this occurs here, and it may be that one would expect it only rarely. In a large series of oral infections of *A. caninum* in dogs the writer found development definitely started on the third day, but never on the second. In cats no cases were found where any change from the infective larval condition was in evidence on the third day, but several cases showed some development on the fourth day.

It is a rather common occurrence that parasites may start to grow in an unusual host but never complete their development. With regard to hookworms this seems to be true in certain cases, but it is more usual that once development has started it is completed. This is shown by the fact that the number of developing worms in the host after experimental infections was found to be a constant percentage of the number of larvae given regardless of the length of time after infection (Scott, 1928). If worms were starting to develop and not completing development one would expect to find a decreasing number of worms as they grew older. This is not true until the worms have completed their growth at least.

There are, however, certain cases in the literature where hookworms have been found to stop growing or to be lost from the host when only partially mature. In most of these cases, however, it has been true either that other observers have found development completed in these hosts or that the search was not continued long enough to insure that development would not have been completed.

A peculiar situation has been found to exist in regard to the growth of the dog hookworm, *A. caninum*, in the cat (Scott, 1929 c). It will be necessary to anticipate somewhat a discussion of the fact that two physiological strains of this species have been found (Scott, 1929 a). One of these is infective to dogs but only slightly infective to cats. To the other strain, however, cats are very susceptible, but dogs are almost entirely insusceptible. When specimens of various ages recovered at autopsy were measured it appeared that regardless of the infectivity of the strain, development was more rapid in dogs than in cats. The final size reached was also less in cats than in dogs by about 20 per cent. In dogs the females of the dog infective strain reached a final size of 12 millimeters in about 30 days. At this time the males had also reached their final size of 9.5 millimeters. In cats, however, the growth continued for a total of 40 days after infection, when the males and females were 8 and 9.5 millimeters long respectively. The cat infective strain apparently had an exactly similar development in these two hosts regardless of their infectivity. We are faced with the fact then that two strains of this species of hookworm which have an inherent difference in infectivity to two hosts have exactly similar growth constants in each of these hosts, but both differ with the host. We shall have

occasion at a later point to discuss more fully the significance of these facts in the biology of the worms.

It is rather interesting also that the curve of growth plotted to these data from parasitic animals was similar to that which has been fitted to a variety of free living organisms. The data show only the growth in the adult stage, that is, after the final moult. Before this moult growth apparently takes place at about the same rate as afterwards. There is probably some discontinuity at the time of moulting, but it must be slight. It has proven rather difficult to make any exact determination of the growth during the early period within the host. The time of passing through the different moults varies so much from host to host that even average figures are unreliable.

REPRODUCTION OF HOOKWORMS

In such a parasite as the ones we are considering, where no asexual multiplication takes place either outside or inside the host, there is frequently an enlancement of the only means of multiplication, i.e., the development of fertilized eggs. Biologically then the number of eggs produced is important in the preservation of the race. From other points of view also, the egg production of hookworms has become a matter of considerable interest. Among these is the importance in the minds of those studying the public health aspect of these parasites of the number of eggs produced daily. The size of an infestation harbored by a person can be estimated by a determination of the number of eggs passed daily provided there is also known the average number of eggs produced by one worm. This knowledge is valuable in turn, since it is a measure of the damage done to the patient, of the danger of the infested person to the community, and for estimating the total infestation

rate of the community. The experimentalist is also interested in the egg production, since it furnishes a convenient measure of the size of an infestation.

Sexual maturity may be determined by two methods. In the first place copulating pairs found at autopsy indicate that it does not occur before the twelfth day in *A. caninum*. Determining the time of appearance of eggs in the feces of the host is another method which does not involve the death of the host. In *A. caninum* this has been found to occur on about the fourteenth or fifteenth day after infection. Herrick (1928) states that this prepatent period was longer in a group of older dogs. In cats (Scott, 1929 c) infested with this same species, eggs did not appear in the feces before the twentieth day. The period averaged 22 days in a number of the latter host. In *A. braziliense*, however, this period was about the same for dogs and cats, averaging 15 days in young animals of either species (Sarles, 1929 a). In old cats, however, the average period was longer, namely 20 days. Old dogs have not been tried extensively. The species parasitic in man take much longer to mature, namely about 40 days.

Determination of the number of eggs laid by the female worms in a given period of time is complicated by a number of factors. In the first place it must be based on counts made of the eggs produced by all the worms in a host. If one could be certain that only one female were present throughout the period studied, the matter would be considerably simplified. The egg output of larger infestations has been shown (Herrick, 1928; Sarles, 1929 c) to rise for a short period of time and then decline. Although the rise is probably due to increasing egg production of the individual worms, it will be shown later that the decrease is probably mostly due to the death of some of the worms. Be-

sides such a variation in the egg production of the worms with their age, it may also vary with the species, size and age of the host. Sarles (1929 c) has shown that the number of worms present in an infestation affects the egg output, there being smaller numbers of eggs produced by the females when present in large infestations than when present in small ones. Besides these variations in the actual egg production of the female worms, there are other variations, such as the output of feces of the host, which make its determination difficult.

As mentioned before, the actual estimates of egg production have assumed considerable importance in public health work, since, once this factor is determined, the process can be reversed and the number of worms present in an infestation can be estimated from the egg output. Estimates of the number of eggs produced daily by females of *Necator americanus* are usually between 9,000 and 10,000 (Stoll, 1923; Sweet, 1925; Hill, 1926). The daily egg production of *A. duodenale* is estimated as considerably more, namely from 20,000 to 25,000 (Soper, 1927; Cort, Stoll and Grant, 1926; Augustine *et al.*, 1928). These estimates from human infestations are based on average natural infestations supposedly containing worms of a wide variety of ages. In the species infesting animals the age can be controlled more exactly. Sarles (1929 c) found that the daily egg production of female *A. caninum* in dogs increased as mentioned above for the first month up to about 20,000 to 25,000 eggs per day. In heavy infestations (over 200 worms), however, this value did not go above 10,000. From this time on he found a decreasing egg production. Herrick (1928), on the other hand, found that in a series of dogs infested with the same strain of worms, the

average egg production increased from 7,000 to 17,000 over a period from 30 to 200 days of age. This difference may possibly be due to the fact that he was dealing with lighter infestations in the older ages.

The length of time over which egg production continues and the length of life of the worms are also difficult matters to determine. This is true mainly because it is absolutely essential to demonstrate that no subsequent infection occurs after the experimental one. Furthermore, about all that can be determined with certainty in regard to the species infesting man is the maximum length of life. Various estimates and determinations have been made but are often invalidated by the fact that the nonoccurrence of reinfestation was not completely assured. About all that is certain is that the maximum life of either species is not usually less than three or four years. Chandler (1925) attempted to measure the length of life indirectly and found that the average egg count of inmates of a well sanitized jail decreased 50 per cent during the first few months after admission. The relation between this determination and the maximum length of life is again not fully known. Sarles (1929 b) found the maximum length of life of *A. caninum* in dogs to vary from 43 to 100 weeks. He found, as had Herrick (1928), that egg output of an infestation decreased rapidly after the first month. Although some of this decrease may have been due to a decreasing production of eggs by the worms, as was mentioned above, it was probably primarily a result of the death of worms. On the basis of these results it might very well be that although Chandler did find such a rapid decrease in egg output in human infestations, maximum length of life was a matter of years.

THE EFFECT OF HOOKWORMS ON THEIR HOSTS

Because of the importance of the disease caused by hookworms there has been a great deal written in regard to their effect on the human host. No attempt will be made here to relate any of the clinical pictures caused by the parasites, but a few of the outstanding points in their effect on laboratory animals will be mentioned and compared with similar effects in man. Chronic hookworm disease causing debility, anemia and loss of weight, such as is common in man, does not appear to be so frequent in dogs. In our laboratory this picture has only seldom resulted from experimental infestations, and these cases were not all entirely uncomplicated. The most common result of an infestation large enough to produce a noticeable effect on the health of the host has been death, usually occurring on about the twelfth day. This is at the time when the worms are growing most rapidly and is probably correlated with blood loss, as will be explained later. Other dogs which had received a few less worms or whose resistance was slightly greater showed symptoms of exhaustion for a few days at about this time and then rapidly recovered and appeared entirely normal throughout the rest of their lives. Visitors to the laboratory have repeatedly been unable to distinguish such dogs from uninfected controls from the same litters. Apparently on an adequate diet a dog is usually able to compensate entirely for the damage done by the worms once it has passed the critical period during the rapid growth stage of the worms. As already mentioned there have been cases where the damage has been chronic, and the dog has been in poor condition for a long period of time. This is the type of damage most familiar to veterinarians, since acute cases would not so often be brought to their attention. Furthermore,

the latter type might not occur very frequently in nature, since there the larvae are probably acquired gradually.

Attempts to measure the damage caused by hookworms have not been attended by a great deal of success. The chief quantitative results have been from studies of blood changes. Many of these studies have been on anemia, since this is the most outstanding feature of the clinical picture of hookworm disease. In the first place the cause of the anemia has received considerable attention. There are three ways in which the anemia may be caused: chronic blood loss, hemolysis and destruction of corpuscles in the blood stream, or a toxic effect on the blood forming organs.

The loss of blood has been calculated at various times, and there seems to be a consensus of opinion that it is not sufficient to cause the effects seen. In the acute cases in dogs mentioned above, however, it can hardly be doubted that blood loss was the important cause of the anemia. The intestine at autopsy was greatly injected, the mucosa bright red and covered with blood, and the lower part filled with clotted and partly digested blood. The stools for several days before death were composed only of blood and mucus. The red blood cell count (Sarles, 1929 c) diminished so rapidly as to suggest that the effects were due to blood loss rather than an effect on the blood forming organs.

This sort of blood loss is not the common picture in chronic cases, however. Sarles (1929 c) shows that the red cell count and hemoglobin of a chronic case in a dog declined and persisted at a level lower than normal. This is apparently similar to the condition in most chronic human cases. In man it has not been possible to follow the blood picture of a chronic case over any considerable period of time, but a large number of determinations of hemoglobin have been made. In practically every case the

hemoglobin index of even moderately severe cases averaged lower than that of non-infested individuals of the same community. The literature on certain phases of this problem has been recently reviewed by Cort, Schapiro, Sweet, Stoll and Riley (1929). This chronic anemia is the picture which does not seem to be adequately explained on the basis of blood loss. Neither do explanations based on hemolysis and destruction of red corpuscles have many advocates. Among other arguments are those of De Langen (1922) who has shown that the bilirubin in the blood is not above normal as it is in chronic malaria; and that the red corpuscles are not excessively fragile.

The remaining explanation is that of a toxic depressing action on the bone marrow and other blood forming organs. The pathology of these organs in chronic cases has not been adequately studied. Furthermore, there is still a possibility that this action is not due to the hookworms themselves, but to a secondary bacterial invasion in the wounds they cause.

Most of the other blood changes are of doubtful significance. The white count is usually high, although it may be below normal in long-continued severe cases. The eosinophiles, however, respond to the invasion of hookworms as they do to many animal parasites. Sarles (1929 e) has made a study of eosinophilia in dogs in order to throw light on the scattered facts recorded in the literature concerning human cases. He found marked changes in adult dogs infected either orally or cutaneously with *A. caninum*. Along with a general leucocytosis there was a pronounced eosinophilia going as high as 42 per cent in one case and persisting for some time. This rise was preceded, however, by a decrease in the number of eosinophiles in the circulating blood

which may indicate a local accumulation and a delayed response of the organs where they are formed. In young dogs, while there was a similar general leucocytosis, the changes in the eosinophiles were distinctly less than in old dogs and appeared to be associated with the production of anemia.

BIOLOGICAL VARIATIONS IN HOOKWORMS WHICH ARE CORRELATED WITH VARIATIONS IN THE HOST

There are a number of variations in the biology of hookworms which are closely correlated with variations in the host, and which appear at least to be the direct result of the latter. Variations may be due to the fact that one species of parasite may frequently be found in more than one species of host, or they may be correlated with the age of the host. Among other host variations which may be suggested but about which little is known are differences in the size of the host, its condition of health, its diet, and the presence of other parasites and diseases.

One of the most interesting cases of variations correlated with host species is found in the situation regarding the hookworms of domestic dogs and cats. This is especially interesting because it has permitted a certain amount of experimental analysis. Two species of the genus *Ancylostoma* are commonly found in these hosts. *A. braziliense* is frequently found in both dogs and cats in certain localities over many parts of the world. It is apparently indiscriminate in regard to these two hosts and passes readily from one to the other. The other species, *A. caninum*, behaves quite differently when tested under controlled conditions. From the results of experimental infestations with the two hosts (Scott, 1929 a) it is apparent that this species does not pass readily from one host to the other.

Larvae from infestations in dogs do not easily infect cats, and it is scarcely possible to infect dogs at all with those from cats.

An attempt has been made to find out something of what this situation means in the biology of this parasite. The most satisfactory hypothesis seems to be that the species *A. caninum* was originally a parasite of dogs. The genus is composed, however, of various species of parasites of both cats and dogs, so that it seems probable that it was also slightly infective to cats. Then by some means a modification occurred in a certain portion of the species so that it became more infective to cats. Apparently in doing this it also became less infective to dogs, so that we now have in existence the two types of strains. A study of the distribution of the species shows that it is much more common in dogs than in cats. Where it is reported for cats it usually occurs in small numbers and relatively infrequently. In certain localities, however, it does appear to be fairly common in cats and occurs in large numbers. A test of one such locality (Scott, 1929 b) showed that worms from cats represented cat infective strains. At the same time a test was made of worms from dogs from a locality where the species occurs in dogs but not in cats. In this case all the strains tested proved to represent strains highly infective to dogs but only slightly to cats. There seem to be at least two possible explanations of how these modifications took place. Although this species is rather rigidly specific to dogs and to cats as explained, it has been recorded occasionally from a large number of other hosts, mostly *Canidae* and *Felidae*. If then we start with the hypothesis that the species was originally a parasite of dogs, it would still be possible to consider that it occurred in other hosts occasionally.

Since man's domestication of animals

and possibly earlier, the domestic cats and dogs have been more closely associated than any other members of their families. This species of hookworm, *A. caninum*, would probably occur then in cats more frequently than in any other host besides its original one. Now it is a possible hypothesis that if the parasite existed and reproduced in a new host for one or more generations, it would become better adapted to that host. On the other hand, it is possible that the occasional specimens found in hosts other than the original one represent variants whose infectivity has been suddenly changed by mutation or otherwise. When both sexes of such variants occurred in a new host, the progeny would represent a new strain infective to that host. Which of these two explanations is true cannot be stated at the present time. Certain further experiments (Scott, 1929 e) have been done to test them, but no final conclusions have yet arisen. Two of the typical strains were introduced into the hosts to which they were not highly infective and the infectivity of their progeny tested after one or more generations. The experiments were not extensive enough to warrant definite conclusions, but it seemed that the dog infective strain did not become any more infective to cats or less so to dogs by having passed from one to three generations in cats. On the other hand the cat infective strain did appear to become more infective to dogs and less so to cats by having passed only one generation in dogs. If our hypothesis that this species was originally a parasite of dogs is correct, it appears that modification to the cat infective condition may have been difficult to achieve or occurred infrequently, but the reverse modification of a cat infective strain back to a dog infective condition was relatively easy. These experiments do not eliminate, however, the possibility of

the change being one of a genetic nature. Other experiments (Scott, 1929 c) have been tried to test this by attempting to produce a cross between the strains in both animals, but so far it has not been possible to do so. The experiments are not extensive enough to determine whether it will ever be possible or not. Other genetic experiments, which will determine the correct explanation of the modification of infectivity, are undoubtedly feasible and should be attempted.

However these variations may have occurred, the facts indicate that at the present time this species, *A. caninum*, occurs in two types of strains which have differing inherent infectivity to two species of hosts. The local distribution of the cat infective type of strain indicates that it has probably originated from the dog infective type at various places and times.

In contrast to these inherent variations in the strains, the characteristics of growth of both types of *A. caninum* are apparently entirely independent of any modifications of infectivity but are dependent on the species of host. Growth does not occur as rapidly and the worms do not reach as great a final size in cats as in dogs (Scott, 1929 c). This is true for both strains regardless of their infectivity. We may assume in connection with our hypothesis that the species was originally a parasite of dogs, that the cat is not as suitable a host as the dog, and for some reason growth is somewhat inhibited in the cat. Even though certain strains have been developed to which the cat is a more suitable host from the point of view of susceptibility, the influence on inhibition of growth is still present. It would be interesting to see how this influence of the host species on the growth would be reflected in the egg production and in other functions.

When we turn to the other species of this genus common to cats and dogs we find quite a different situation. *A. braziliense* shows no evidence that it was ever primarily a parasite of one species of host or the other. No differences in strains have been detected, and larvae from infestations in either host are infective to both species. Growth has not been measured adequately, but a few observations are recorded (Sarles, 1929 a). These available measurements indicate that growth may take place slightly faster in dogs than in cats, but the difference is not significant, and the similarity of the pre-patent periods in the two hosts shows that there can be no such difference as is the case with *A. caninum*. Although we have no evidence to explain how it occurred, it seems that this species, *A. braziliense*, has become adapted equally well to life in cats and dogs.

Another important variation in the host which influences the parasite is the age of the host. We have continually mentioned various influences of this factor, and it may be well to recapitulate them here. The most noticeable effect is what has been called age resistance. With the species *A. caninum* and *A. braziliense* in both cats and dogs there is a definitely decreasing susceptibility correlated with advancing age of the host. As an example there may be cited variation with the age of the host of the percentage of larvae given by mouth which develop to maturity. Herrick (1928) found that in young pups an average of 35 per cent. of the larvae of *A. caninum* developed, while in mature dogs only three per cent. developed. This was the dog infective strain, which is scarcely infective to cats, but even with this, more developed in kittens than in mature cats (Scott, 1928). The cat infective strain (Scott, 1929 a) showed the same difference more markedly

in this host, an average of 45 per cent. developing in kittens, while a much smaller percentage developed in cats. With *A. braziliense* the same was true in both cats and dogs. Sarles (1929 a) reported that an average of 32 per cent. developed in a series of young cats while only four per cent. developed in adult cats. Likewise he found a correlation with the age of dogs, 44 per cent of the larvae developing in puppies and five per cent in adult dogs. Although such exact experimental work cannot be done with the human host it seems fairly obvious that no such correlation with age can be true for either species infesting man. Epidemiological studies have shown that in practically all regions children have fewer hookworms than adults. In the few cases where children are more heavily infested than adults, the difference seems to be correlated with the habits of the two age groups. Many extremely large infestations do occur in adults, which would be quite unlikely if there were such a difference in susceptibility with age as is found in the other species.

Other effects correlated with the age of the host have been noted. The skin reaction of old dogs, in contrast to that of young dogs infected with larvae of *A. caninum*, has already been described. Although further work along this line is needed, it seems almost a certainty that this difference was correlated with the age of the dog and not with previous infestation. It has also been mentioned that in the same series (Sarles, 1929 c) the old dogs showed an eosinophilia much more marked than that in young dogs. A study of the growth of *A. caninum* showed no correlation between the length of the worms and the age of the host, although it is not improbable that more extensive series might do so (Scott, 1929 c). On the other hand, both this species (Herrick,

1928) and *A. braziliense* (Sarles, 1929 a) seem to require longer to come to sexual maturity in old than in young hosts. There are so many other variables to consider in a study of egg production that it has not been possible to determine whether this function varies with the age of the host.

IMMUNITY TO HOOKWORMS

That the substitution of the words susceptibility and insusceptibility for the terms immunity and resistance in referring to animal parasites is a practice to be preferred, is an opinion which the writer has previously expressed (Scott, 1928).

The word immunity, for example, has for the most part, been applied in bacteriological work to that phase which has so far been of the greatest medical significance, the development of acquired immunity. . . . Furthermore the word resistance is apt to produce the unconscious impression of the presence of factors in the host actively antagonistic to the parasite or its effects.

There is another caution which should be observed in using terms which are common in bacteriological parlance, that is we must clearly distinguish between the insusceptibility to the effects of parasitism and the insusceptibility to the colonization of the host by the parasite. The writer has mentioned this matter before (Scott, 1928) and can do no better than to repeat.

In the case of parasitism with most helminths it is possible to distinguish quite readily between colonization of the host by the parasite on one hand, and the effects of parasitism on the other. In bacteriological work this distinction has frequently been omitted. From a medical point of view the effects on the host are often of predominant interest. In many cases it is difficult to distinguish between resistance to colonization and to its harmful effects. Cases of the natural insusceptibility of a species or race to the toxic products of bacteria are known. Kolmer (1923) cites a number of cases where antitoxin apparently exists in an insusceptible species of animal, and where toxic products, when produced, find no suitable receptors in

the cells of the host. Schwartz (1921) has shown that *A. caninum* produces a nonspecific hemolysin and that normal serum has antilytic properties which inhibit the action of this hemolysin. It may be then that the situation in regard to the susceptibility of the host to the effects of the parasite will be found to be quite parallel in bacteriological and helminthological parasitism. Our interest is, however, not so much in the insusceptibility of hosts to the effects of parasitism as in their susceptibility to colonization by the parasite.

There are several kinds of reactions which may come under the term insusceptibility to infestation with regard to the hookworms. In the first place, there is what may be called racial immunity or species insusceptibility. We have seen that the hookworms are relatively specific. In other words only one or two hosts are ordinarily suitable for the development of each species, but rarely a number of other hosts may be sufficiently suitable to allow a few to grow. It seems as though a knowledge of what happens to larvae introduced into these hosts in which they do not ordinarily develop might possibly help to explain the mechanism of other types of immunity as well. One fact of considerable importance has been learned from work which the writer has been pursuing along this line. If the larvae which are introduced into a host are unable to grow they tend to remain in the host in the same condition in which they were introduced. The significance of this phenomenon will be discussed later, since it has been found to occur also in other types of insusceptibility.

Insusceptibility correlated with the age of the host has already been discussed in the previous section, and we may consider next the immunity due to the presence of a previous infestation. Carefully controlled experiments to determine whether there is any inhibition to the development of larvae introduced while a previous infestation is still present are

greatly needed. Those which have been recorded are somewhat inconclusive on this point. Herrick (1928) found that a second infestation given while the first was still present was just as large in proportion to the number of larvae given as was the first. In some cases infestations did seem to be a little smaller when two or three previous infestations had been given and were still present. The method of measuring the size of the infestation based on the egg output was quite variable, and he interprets his results with caution. Decreasing susceptibility due to advancing age of the dog during such an experiment is apt to mask the result. It is certain, however, that if such an insusceptibility is demonstrated it will not be absolute and probably will not be of any great degree.

Another consideration which has frequently been mentioned is whether insusceptibility to infestation results from the presence of worms of other species. The question has been raised in a number of cases where the facts cannot be easily explained on other grounds. Sarles (1929 a), for example, records a case of a dog which failed to take an infestation of *A. braziliense* which on the basis of previous work should have been established. The presence of a large infestation of *A. caninum* was the only factor which differed from other cases in the same series which did take an infestation. Other similar cases frequently come to notice and indicate that a series of experiments should be performed to clear up the question as to whether this insusceptibility is due to some extraneous factor, or in case it is due to the presence of another species, how frequently it occurs and under what conditions.

What is usually termed acquired immunity should be distinguished from the above immunity due to an existing infestation,

since in this case the insusceptibility arises from the fact that the animal has had a previous infestation, but it is no longer present. We have no evidence that there is any such phenomenon in the case of the hookworms. In a series of experiments Herrick (1928) showed that there was no reduction in the size of an infestation of *A. caninum* established in dogs where previous infestations had been present but cleared out by anthelmintics.

THE MECHANISM OF IMMUNITY

No study of immunity or insusceptibility is complete without a consideration of the mechanism involved. Few immunological mechanisms have been carried beyond the stage of hypotheses. In the case of insusceptibility to parasitic worms no widely accepted hypothesis has been proposed and very little has been done toward establishing any hypothesis that has been suggested. Preliminary to a study of the mechanism of immunity there must be a determination of the conditions under which various types of insusceptibility occur. The hookworm problem is rapidly reaching the point where it is safe to consider that these conditions are roughly outlined and already some observations bearing on an explanation of the insusceptibility have been made.

There is a possibility that a local immunity is developed in the skin of animals which prevents penetration twice in the same area. Moreover, it is conceivable that this immunity could spread from a localized area and cover the whole skin. Its action would probably not be that of preventing actual penetration, but that of killing or inhibiting the larvae after they were in the skin. No extensive attempts have been made to determine whether such an immunity exists. Sarles (1929d) found a peculiar situation in old dogs insusceptible to infestation and in which the

marked cutaneous reaction described above followed the penetration of the skin. From these areas live larvae were recovered for a period of 60 days in some cases, and in all cases they persisted much longer than in young dogs in which no cutaneous reaction occurred. Sections of the area showed that many larvae were present, some apparently alive, and some dead and surrounded by a cellular infiltration. Further histological work on experimental animals should help elucidate the mechanism of any cellular reaction which may be important in whatever immunity is developed. It should also be possible with the proper technique to demonstrate the presence of any antibodies which might be developed against the larvae.

It has been repeatedly demonstrated (Scott, 1928; Sarles, 1929 a) that after an infection by skin or by mouth of even entirely insusceptible hosts, the larvae can be found alive in the intestine. This was made possible by the use for recovering larvae from various tissues of the host of the Baermann isolation apparatus, which was previously used for isolating larvae from the soil. The most fundamental point in the immune reaction must come in the intestine, and the critical point for the parasite is in being able to initiate development. Certainly it is not primarily a matter of the insusceptible host destroying the parasites. A series of experiments involving both normal and abnormal hosts (Scott, 1928) have shown that regardless of whether few or many worms developed, there was usually a residual number which did not. These larvae which did not develop were recovered alive in considerable numbers from the same place as were those which did develop. For example, a cat was infected with larvae of the dog strain of *A. caninum*. After 44 days the animal was killed and found to harbor a few mature worms

which had resulted from the infection given. At the same time larvae were recovered from the intestine entirely undeveloped and in exactly the same condition they were in when they were introduced. Similar larvae were found in rats where none were developed, and in dogs where a large number had developed.

The question which now presents itself is: Why did these larvae not grow? In some cases from the same group of larvae introduced into various animals, many were found undeveloped in rats and none developed, in cats a few were developed and many undeveloped but alive, while in dogs most of those given were developed but a few were unchanged. Why did varying numbers grow in different hosts? Certainly not because of a difference in the larvae, for they were all from a common source. Furthermore, it was demonstrated that those which did not develop were not incapable of development. They were removed from these various hosts and introduced into other hosts of the same or different degrees of susceptibility. Here the percentage development was exactly the same as would have been postulated for the particular host infected with newly cultured larvae. Even here, however, a certain percentage would not develop, but remained unchanged as before. In one case some of this group were again transferred to a third host and the usual percentage developed. In other words the larvae were apparently all potentially able to develop, but certain host conditions determined what percentage developed in each case. What are the necessary conditions in the host, is now the crucial question. It may be that the host inhibits the development of all but a certain number of the larvae. Or it is just as likely, or perhaps more so, that certain peculiar conditions are necessary for development and the degree to which these conditions are

fulfilled determines the percentage which can develop.

This hardly seems to be anything like the situation in bacteriological immunity, where certain antibodies are supposed to prevent the normal growth of the organisms. Here we have one host in which none of the parasites grow, another in which few grow and still another species in which many grow. In all of these, however, some of the parasites do not grow, but they do remain alive in the host and are entirely capable of development if transferred to another host. In hosts where susceptibility varies in accordance with age the same phenomenon occurs, and again the situation is still more complicated by the fact that the conditions in two hosts are exactly reversed when a different strain of parasite is used. The situation is not simple, then, and it hardly seems possible that any hypotheses which have been suggested for other organisms will account for these facts.

PRESENT PROBLEMS IN THE BIOLOGY OF HOOKWORMS

At every point in our discussion there have arisen many unsolved problems, some of which may now be collected here together. We have seen that a great deal of information has been gathered in regard to the distribution of the various species and their specificity to various hosts. But continued observations will undoubtedly bring to light new facts, and especially should the distribution of various host strains be more adequately studied.

Although skin penetration was discovered so long ago and a great deal of work done since, we are still far from being able to explain all of the biology of the larvae involved in skin penetration. The reaction of the host to skin penetration is connected so closely with what may be immune reactions that we may consider

the former to be a part of the latter problem. Migration from the skin and after oral infection is not adequately described. Why do larvae remain in the skin longer in old dogs than in younger ones? Do they also remain longer in the skin of other insusceptible animals? We have seen that after oral infections migration does not usually occur in normal hosts, but in abnormal hosts it has been recorded under certain conditions. What are the factors which cause this difference? Do they have any bearing on the subsequent development of the parasite? We have seen that the study of the growth of hookworms has demonstrated that in the adult stage they follow growth curves similar to those of free living animals. The most significant variation is apparently due to the species of the host. This should be investigated to determine the mechanism involved. Furthermore other variations possibly correlated with variations in the susceptibility of the host will doubtless appear. A study of the growth during earlier stages is difficult technically, but not impossible, and may give clues to other biological facts of importance.

Egg production will undoubtedly be studied further. It is our sole method of estimating the size of infestations. Its importance to experimental and practical work will require that the variations be more adequately defined. Although these practical considerations may be uppermost in the mind of the investigator, our knowledge of the biology of the parasite is bound to advance.

We have only begun to study the effect of hookworms on the host. Even the pathology of well recognized clinical manifestations is relatively unknown and future work involving the pathology of the physiological reactions of the host ought to be fruitful. Furthermore, little

has been done toward studying the balance of relations between the host and the parasite. We know only a few variations in the parasite which seem to be caused by variations in the host, and practically nothing of the factors involved. The relation of the physiological strains already described and the other possible ones offers a very attractive field. If it is a genetic matter, an experimental attack ought to elucidate the problem. If it is not, an attempt to produce modifications should be of great value.

The immunological relations of the host and parasite are also practically an untouched field. In the first place we need to know more of the facts of insusceptibility. Is there any immunity due to the presence of a previous infestation? Is there any due to a previous infestation which has been lost? How rapidly does the insusceptibility increase with the age of the host? Then the mechanism is entirely unknown. As already pointed out, significant results will undoubtedly come from the application of methods which have been useful in bacteriological immunology. The facts known at present, however, indicate that the inhibition through the production of antibodies may not be as important as it is in bacterial reactions. We certainly know that hookworms are not killed by the insusceptible host, but remain in it alive and capable of development. What are the factors necessary for this development? This is probably the most crucial question we have to face at the present time.

This paper is a contribution from the Department of Helminthology of the Johns Hopkins University, School of Hygiene and Public Health, supported by a grant from the International Health Division of the Rockefeller Foundation. The writer wishes to thank Dr. W. W. Cort and members of his department for aid in consultation and criticism.

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NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of THE QUARTERLY REVIEW OF BIOLOGY, 1901 East Madison Street, Baltimore, Maryland, U. S. A.

BRIEF NOTICES

EVOLUTION

EMERGENT EVOLUTION AND THE INCARNATION. *Washington Cathedral Series.*

By William C. Woods.

*Morehouse Publishing Co.
Milwaukee*

\$1.00

$4\frac{1}{2} \times 6\frac{3}{4}$; x + 109

Here is a striking proof that in this generation the children of light are as up and coming as the children of this world: emergent evolution, now so fashionable among philosophically minded biologists, serves in this book as a buttress to orthodox Christian theology. Dr. Woods knows far more about theology than most biologists and far more about biology than most theologians. If then his argument is not altogether convincing, the fact may be taken as an index of the intellectual difficulties of reconciliation.

Like most writers on the subject, Dr. Woods considers the virgin birth of Jesus as a unique event. This is by no means justifiable. There are a number of cases of virgin birth in the literature, some of them in America. Thus among the Algonquins Manibozho, among the Hurons Joskeha, among the Mexicans

Quetzalcoatl and Uitzelopochtli, among the Peruvians Viracocha, were all virgin born. Yetl, a tribal hero of the Thlinkeets of North Western America, was conceived as a result of his mother's swallowing a pebble and a draught of seawater on the advice of a friendly dolphin. The conception of Jurapari of the Brazilian Uapès was the result of his mother's drinking fermented liquor. In many other instances conception has followed the use of fermented liquor, but these are not properly speaking cases of virgin birth, the liquor not being the proximate cause of the conception.



WHAT IS DARWINISM?

By Thomas Hunt Morgan.

W. W. Norton and Co., Inc.

\$1.00

$4\frac{1}{2} \times 6\frac{3}{4}$; 78

New York

In this reprint, with additions, of his article in *The Yale Review* Morgan considers the bearing on the theory of natural selection of later developments in genetics, especially Johannsen's work on pure lines and the various researches on mutation. While admitting the force of Bateson's objection that infertility has not been observed between a mutant and its parent

type, he concludes that Darwin's argument for organic evolution "is as cogent and convincing today as it was nearly seventy years ago." In the second part of the book Morgan replies to J. S. Haldane and A. V. Hill on the sufficiency of a mechanistic interpretation of self-regulating organisms. In these days of triumphant mysticism it is pleasant to find a distinguished biologist who is still a staunch mechanist.



THESE MISSING LINKS; *Comments on Human Evolution.*

By Francis P. LeBuffe. The American Press
10 cents 5 x 7½; 32 (paper) New York

This little pamphlet contains a collection of short papers in which the author, a member of the Society of Jesus, attacks the views of those anthropologists and ethnologists who seek to prove the evolution of the human species from lower forms. He refuses to see any evidence that in primitive man, either of existing tribes or in ancient remains, can be found any of the so-called missing links between the higher anthropoids and *Homo sapiens*. He quotes freely from the writings of Osborn, Gregory, Hrdlička, Burkitt, Elliot Smith and many others, including a number of Catholic writers. Naturally, he carefully selects his material to prove his point.



ORIGIN THROUGH EVOLUTION.

By Nathan Fasten. Alfred A. Knopf
\$3.75 trade edition 5½ x 8; 456 New York
\$3.00 text edition

A pedagogic presentation for the layman and beginning student of the general idea of evolution in nature and the evidence which supports its acceptance by scientists. Both organic and inorganic evolution are

dealt with and modern physical theories and general biology reviewed on the way. So large an undertaking in so limited a space is necessarily bound to be somewhat superficial. However, for its intended purpose, an elementary textbook, it is excellent. Glossary and index are provided.



GENETICS

PLANT HYBRIDIZATION BEFORE MENDEL.

By H. F. Roberts. Princeton University Press
\$4.00 5½ x 8½; xiv + 374 Princeton, N. J.

This volume will be extremely useful to all students of genetics. The title is somewhat misleading. While a large part of the book is devoted to pre-Mendelian work, the author includes the work of Gregor Mendel and of those investigators who rediscovered his law. The presentation of the subject is historical rather than genetic in character. The aim of the author is to present the work of all investigators who have contributed in some manner to the theory of fertilization and hybridization in plants. Besides very thoroughly analyzing the important researches in this field he includes many quotations from the original papers. He thus brings into relief the important steps in the development of the genetic theory and rescues from obscure sources many interesting details of historical interest which might otherwise be lost sight of. Special chapters are devoted to the researches of Kölreuter, Darwin, Galton, Mendel, and Bateson, while in chapter XI will be found an excellent presentation of the subject matter in the papers of DeVries, Correns and von Tschermak on the rediscovery of Mendel's law. Added interest is given the book by numerous

illustrations, including photographs of many of those who have been pioneers in the hybridization of plants. Each chapter concludes with a list of references. The book is well indexed, while under a special heading is given a list of hybrids by genera of their parentage, and of genera made the subject of experiment.



HANDBUCH DER VERERBUNGSWISSENSCHAFT. *Lieferung 6. Band I. Fortpflanzung und Befruchtung als Grundlage der Vererbung.*

By Max Hartmann. Gebrüder Borntraeger
9.60 marks (Subscription) Berlin
19.20 marks (Single copies)

7 x 10 $\frac{3}{8}$; 103

HANDBUCH DER VERERBUNGSWISSENSCHAFT. *Lieferung 9. Band II. Verteilung, Bestimmung und Vererbung des Geschlechts bei den Protisten und Thallophyten.*

By Max Hartmann. Gebrüder Borntraeger
12 marks (Subscription) Berlin
24 marks (Single copies)

7 x 10 $\frac{3}{8}$; 115 (paper)

HANDBUCH DER VERERBUNGSWISSENSCHAFT. *Lieferung 7. Band II. Artbastarde bei Pflanzen.*

By O. Renner. Gebrüder Borntraeger
14 marks (Subscription) Berlin
28 marks (Single copies)

7 x 10 $\frac{3}{8}$; iv + 161 (paper)

The first two of these parts of this great handbook of genetics, by one of the editors, Dr. Max Hartmann, put heavy emphasis on the cytological aspects of the problems of reproduction and fertilization, and the determination and inheritance of sex in primitive plants and animals. They are abundantly illustrated and carry sufficiently extensive bibliographies. Renner's part on species hybrids in plants is an extremely thorough, interesting and useful review of knowledge in this field, in which he is an outstanding worker.

GENERAL BIOLOGY

GENERAL SCIENCE for Reviews.

By W. Dean Pulvermacher and Charles H. Vosburgh. Globe Book Co.

50 cents 5 x 7 $\frac{1}{2}$; 168 (paper) New York

This textbook for general science courses in elementary and secondary schools gives in "a simple clear style, not beyond the intelligence of the average student," a mixture of physics, chemistry, astronomy, meteorology, physiology, botany and hygiene. Here the unsuspecting child learns that alcohol

(1) Lessens physical activity. (2) Lessens skill. (3) Decreases resistance to disease. (4) Increases nervousness. (5) Has a harmful effect upon the offspring. As to its effect upon the separate organs of the body (1) it causes the digestive juices to flow more freely at a time when not needed, (2) it burns the lining of the stomach, (3) decreases the effectiveness of the white corpuscles, i.e., of their ability to resist bacteria, (4) hardens the walls of the arteries (arteriosclerosis), (5) causes the brain center that controls the smallest arteries to lose its control over these arteries. They relax and flood the capillaries going to the surface of the body with blood. This gives the effect of warmth but the body is really losing heat too quickly, (6) the skin is thus flooded with blood and doesn't act properly as a regulatory organ, which it ordinarily does by allowing more blood to the surface in order to pour perspiration on the skin when one is too warm. If one is too cold the tiniest arteries to the surface are closed and blood is not allowed to get to the skin. The center controlling this action is numbed by alcohol, (7) it causes hardening or cirrhosis of the liver, (8) the nervous system gradually breaks down, the higher centers involving the better traits first and finally in the last stages delirium tremens, (9) the muscles are keyed up to a greater effort for a short time but the reaction is such that the average work done is less, and it is for that reason and because of the fact that the muscular ability will soon be lessened, that trainers do not allow athletes to drink alcohol.

Demonstration. To show the effect of alcohol upon protein add some alcohol to white of an egg and note the hardening effect, then add alcohol to spirogyra plant and note that when placed under the microscope the protoplasm within the cells is contracted.

That alcohol, in the dilutions commonly ingested by civilized persons, might have a different effect than when poured undiluted on egg albumen is not suggested.



LABORATORY AND FIELD ECOLOGY.

The Responses of Animals as Indicators of Correct Working Methods.

By Victor E. Shelford.

The Williams & Wilkins Co.

\$10.00 6 x 9; xii + 608 Baltimore

In this book Professor Shelford has made a monumental and encyclopedic contribution to the methodology of animal ecology. It was begun ten years ago with the intention of describing the author's equipment only. Since then the plan has broadened, until in the end more than half the book is devoted to the presentation of ecological data and results. The range and thoroughness of the treatment is indicated by the chapter headings: Some problems of ecology and climatology; methods and results of biotic observation and experimentation; behavior and acclimation; food and food effects; soil and the growth of food plants; dormancy and other quiescent states; animals in relation to temperature; control and measurement of temperature; ventilation under experimental conditions; control and measurement of moisture; temperature and humidity in combination; the effect and measurement of air pressure and evaporation; light conditions and effects; measurement and control of light; the evaluation of factors other than temperature and moisture, and the comparison of species; location and planning of buildings and equipment for the simulation of climatic conditions; physical conditions in water (except light); light conditions in water; chemical conditions in water; location and

planning of buildings for the simulation of aquatic conditions.

There is a bibliography of over 1000 titles, and a detailed index.



A BIBLIOGRAPHY OF AMERICAN NATURAL HISTORY. *The Pioneer Century, 1769-1865. The Role Played by the Scientific Societies; Scientific Journals; Natural History Museums and Botanic Gardens; State Geological and Natural History Surveys; Federal Exploring Expeditions in the Rise and Progress of American Botany, Geology, Mineralogy, Paleontology and Zoology. Vol. III. The Institutions Founded or Organized between 1845 and 1865. Bibliography of Books. Chronological Tables. Index of Authors and Institutions. Addenda to Volume I.*

By Max Meisel. *The Premier Publishing Co.*
\$7.50 6 x 9; xii + 749 Brooklyn, N. Y.

Mention has been made in a previous issue of THE QUARTERLY REVIEW OF BIOLOGY of the first two volumes of this highly useful work on American natural history. The present volume, prepared with the same painstaking thoroughness that characterized the preceding volumes, covers the last twenty years of the "pioneer century." In addition to the bibliographical studies of those institutions founded between 1845 and 1865, chronological tables, etc., the volume contains a bibliography of books and miscellaneous articles on natural history published separately or in serials of institutions not considered individually in the bibliography proper. An amazing amount of material, much of it from inaccessible sources, has been collected and skillfully arranged within the three volumes of this work. It is a valuable contribution to the history of the development of biological sciences in America.

MODERN BIOLOGY. *A Review of the Principal Phenomena of Animal Life in Relation to Modern Concepts and Theories.* By J. T. Cunningham. E. P. Dutton and Co. \$3.00 5½ x 8½; xii + 244 New York

The author believes that modern genetics as it appears in the gene theory of T. H. Morgan, and the mechanistic principles of modern biologists generally do not explain many facts of biology. He cites what he considers are important objections, and belabors the authors of opposing views with great energy, though his own harmonic-vitalistic brand of Lamarckian eye-water has failed to attract any considerable body of followers, in spite of the fact that it has been in the field for a long time. Cunningham's writings are always interesting. The not negligible amount of valuable material they contain would probably gain more respectful attention and exert more influence if their whole viewpoint were somehow less wrong-headed and intolerant.



HOLIDAY POND.

By Edith M. Patch. The Macmillan Co. \$2.00 7½ x 8; 147 New York

We can imagine no more delightful way for a child to get its introduction to natural history than by following the adventures of Rana, the yelping frog, of Lotor, the raccoon, of Picta, the painted turtle, of Sandy, the swallow, and of the other creatures that Dr. Patch writes about.



GRUNDLINIEN DER EXPERIMENTELLEN PLANKTONFORSCHUNG.

Die Binnengewässer Band VI. By Einar Naumann.

E. Schweizerbart'sche Verlagsbuchhandlung
10 marks (paper) Stuttgart
11.50 marks (cloth)

6½ x 10; ix + 100

Another number in the series on *Binnengewässer* of which some have been previously noted in this REVIEW. It deals with laboratory methods for the cultivation and experimental investigation of plankton.



AMERICAN CHEMISTRY. *A Record of Achievement. The Basis for Future Progress. Second Edition.*

By Harrison Hale. D. Van Nostrand Co. \$2.50 5 x 7½; ix + 255 New York

The second edition of a brief and elementary account of the part played by chemistry in the great American industries. Two chapters have some biological interest (Water and Sewage, Sanitation and Medicine; Food).



HUMAN BIOLOGY

IMMIGRANT FARMERS AND THEIR CHILDREN.

By Edmund deS. Brunner.

Doubleday, Doran and Company, Inc. \$2.75 Garden City, N. Y.

5½ x 8½; xvii + 277

The economic, social, and spiritual status of the immigrant farmer and his children is here set forth in considerable detail. Since one-fourth of the foreign-born population in the United States is dwelling in rural areas, a survey of the general immigrant population can hardly be considered complete without such a study. We find nothing alarming in these pages. On the contrary, the fears of the Nordic-minded should be somewhat allayed, if such a thing is possible. Such subjects

as of what nationality are the immigrant farmers, where are they living, are they succeeding in their chosen occupations, are they tending to become standardized American citizens, with whom are they marrying, and can their children compete successfully with the native-born children are discussed. The second part of the report consists of studies by different individuals of four widely separated communities of immigrant farmers, each group presenting its own problems. Particularly interesting is the history of the colony known as Castle Hayne, where, more or less by chance, there collected "Hollanders, Poles, Italians, Danes, Hungarians, Russians, and all other misfits who happened along." That the bringing together of these diversified types caused the melting pot to boil with considerable vigor the history of this colony discloses. There are given in appendices data and tables on naturalization from a special census tabulation of foreign-born in 177 villages, on intermarriage, on distribution of the immigrant farmer by states, etc. There are also charts of intelligence tests of children, and maps of distribution of the foreign-born farmer. The book is well indexed.



MODERN SCIENTIFIC KNOWLEDGE OF NATURE, MAN, AND SOCIETY.

By Frederick A. Cleveland with Collaborators.

The Ronald Press Company

\$4.50 5½ x 8½; xvii + 592 New York

The Ronald Press has evidently concluded that the potential bond salesman or junior executive needs something in his college curriculum wider in its outlook than accounting or principles of salesmanship. Hence this textbook for an orientation course, by the Professor of United States Citizenship of Boston University

and fourteen collaborators, among whom we note the names of F. H. Giddings, H. H. Newman, H. M. Parshley, and Harlow Shapley. It is, of course, impossible to give a really adequate résumé of our knowledge of nature, man and society in 592 pages, but at least the student will get some idea from the book of what the various sciences are about, the concepts that they find useful in dealing with their segment of human experience, and their chief conclusions. There are copious references appended to the chapters, but we fear that if the student aspires to a high grade in his course in accounting he will have little time to explore the sacred jungles of the sciences.

In reading the book one cannot help being struck by the difference in the present state of the physical and biological sciences on the one hand, and of some of the social sciences on the other. Physics, chemistry and biology have by no means solved all their problems, but although they do not know just where they are going, they have a fairly good idea of how to get there. The pessimism of some physicists may be diagnosed, we believe, as a temporary *Bauchweh* caused by a plethora of as yet undigested facts. In the social disciplines the anthropologists and some, at least, of the economists and sociologists have attained to a method which promises to lead them somewhere, but most of the *Gelehrten* in jurisprudence and political science have, apparently, not yet heard the news that Thomas Aquinas is dead. If these disciplines are ever to find their way out of the mediaeval slough in which they are floundering, it will be, we believe, through such work as that of Malinowski on the juridical aspects of anthropology and as that promised by the programs of the institutes for legal research at Yale and Johns Hopkins.

BIBLICAL ANTHROPOLOGY *Compared with and Illustrated by the Folklore of Europe and the Customs of Primitive Peoples.*

By H. J. D. Astley. Oxford University Press
\$4.50 5½ x 8½; 262 New York

This scholarly and well written book covers somewhat the same ground as Sir James Frazer's *Folk-Lore in the Old Testament*, but in less detail. It consists of a series of essays, most of which had previously appeared in periodicals; they are now revised and enlarged to form a continuous study in anthropology as throwing light on many otherwise obscure passages in the Bible and on survivals among the Hebrews of primitive ideas, such as animism, totemism, magic, and tree- and pillar-worship. Thus the stoning of Achan for taking of the spoils of Jericho and the smiting of Uzzah for touching the ark of Yahweh are examples of tabu; the pig is really a totem animal; the two pillars, Jachin and Boaz, set up by Solomon before his temple find their counterpart in the sacred pillars of the Phoenician and Cretan temples. The motto of the book might be the following passage from Driver, which is quoted with approval:

The general result of the archaeological and anthropological researches of the past half-century has been to take the Hebrews out of the isolated position which, as a nation, they seemed previously to hold. . . . Their beliefs . . . their social usages . . . their religious institutions can no longer be viewed, as was once possible, as differing in kind from those of other nations, and determined in every feature by a direct revelation from Heaven; all, it is now known, have substantial analogies among other peoples.

This is a shocking book for a Vicar of East and West Rudham and Honorary Canon of Norwich to write. If any stray Fundamentalist happens to read it, he may well offer a solemn thanksgiving to Yahweh that *his* Pastor knows nothing of anthropology, either biblical or profane.

RESEARCH RECOMMENDATIONS OF THE SECOND CONFERENCE ON PROBLEMS OF THE DEAF AND HARD OF HEARING, Washington, D. C., February 1 and 2, 1929. *Reprint and Circular Series No. 88. Issued under the Auspices of the Division of Anthropology and Psychology of the National Research Council.*

National Research Council
50 cents Washington

6¾ x 9¾; iv + 53 (paper)

This report is the outcome of the work of the Committee on Tactual Interpretation of Oral Speech and Vocal Control of the Division of Anthropology and Psychology in the National Research Council presented to the Division May 1927. The early studies of the committee indicated that it was advisable to make a survey of the research needs and opportunities in the whole field of the care and training of the deaf. A committee was organized under the chairmanship of Dr. Knight Dunlap, and presented its results at the First Conference in January 1928. It was realized then that more information concerning basal problems pertaining to the deaf was needed and, accordingly, the National Research Council appointed a committee of six members under the chairmanship of Dr. Rudolph Pintner to study the problem further. The results were presented at a Second Conference February 1 and 2, 1929, and constitute this report.

The recommendations are categorized under the heads: Surveys; problems of sensory stimulation; educational problems; measures of capacity and achievement; problems of infancy and early childhood; problems of emotional and social adjustment; problems of causation and prevention; research personnel and provisions. For each of these a series of subdivisions lists the suggestions in detail.

THE PHYSICAL BASIS OF SOCIETY.

By Carl Kelsey. D. Appleton and Co.

\$3.50 5 x 8; xxii + 526 New York

An entertaining book for the lay reader who is interested in the general aspects of the relationship of man to his natural environment. As reading matter for the student of sociology this book must be of great value. A first edition (published in 1916) which the author describes as being "little more than lecture notes" in which the reader "bumped along from fact to fact," has been entirely rewritten and very much enlarged. The material, which has been drawn from many widely different sources, is skilfully presented. There is no attempt to force theories upon the reader. Rather, the author holds to a clear statement of the essential facts which investigation has thus far revealed. In brief, it may be said that the book gives a comprehensive survey of society as it is controlled by nature and as it controls nature, of investigations concerning the evolution and inheritance of man and the problems of society which have developed because of man's progress. Of special interest are the chapters on "Sex and society" and "Race differences." Each chapter concludes with a list of books and papers referred to in the text, while there is a lengthy list of suggested readings at the end of the book, and subject as well as name and source indices.



URSPRUNG UND VERBREITUNG DES MENSCHENGESCHLECHTS. Eine Neubegründung des Darwinismus auf Grund der Polwanderungen und im Anschluss an die Theorie Wegeners.

By Franz Koch.

Gustav Fischer

11 marks (paper)

Jena

13 marks (bound)

6½ x 9½; vii -- 174 + 15 plates

According to Dr. Koch, Wegener's theories of continental drift and wander-

ing of the poles explain not only the distribution, but also the origin, of species. As the poles changed their position and the climate of a given area changed accordingly, the members of any species inhabiting that area were faced by three alternatives: (1) to migrate, (2) to adapt themselves to the changed conditions, (3) to become extinct.

Dr. Koch is suffering from a bad attack of patriotism. The whole treatment of human types finds its climax in a dithyramb on *Deutschlands Mission*. The Germans, it appears, wedged in between the "passive fatalism" of the Russians and the "hypocritical and cold hearted energy of the Anglo-Saxons, whose goal is the conquest of the world, and to whom one might say, alas!—Nietzsche's phrase 'the blond beast' applies almost uniquely," compel the unwilling admiration of the world by their science and technology, their philosophy and art, their poetry and music, but reap a harvest of aversion, envy and ingratitude. So long as the North pole keeps in its present position and the Germans breed from their Nordic elements, the cultural advancement of mankind will depend on them. "A cessation of their creative activity would mean the triumph of Russian dullness or of Anglo-Saxon mediocrity—both dismal prospects."



THE STORY OF RELIGIOUS CONTROVERSY.

By Joseph McCabe (Edited, with an Introduction by E. Haldeman-Julius).

The Stratford Co.

\$5.00 6 x 9½; xviii + 623 New York

Why do publishers think it good policy to print the extravagant puffs now customary on the jackets of their books? For our part, when we read that a book is "by far the most scholarly, the most readable and the most fascinating book on

religion since Sir James G. Frazer's 'Golden Bough,' " and that its author is "one of the three greatest scholars in the world today," we open the book in a more Missourian state of mind than we should if the blurb had contained fewer superlatives. Although Mr. McCabe's book scarcely deserves such hyperbolic praise, it is an interesting and well-written account of comparative religion and ethics and of the history of the Christian church. The standpoint is frankly controversial, but the author seems to be an honest fighter. It is well for us to be reminded now and then that organized religion, even the Christian religion, is not all brotherly love and good works.



THE JEWS IN THE UNITED STATES, 1927. *A Study of Their Number and Distribution.*

By Harry S. Linfield.

The American Jewish Committee
New York

Limited edition; free distribution

5¼ x 8; 111

A report of a survey, far more extensive than any hitherto attempted, on the number and distribution of Jews in the United States, made under the auspices of the American Jewish Committee. Not only were data collected on their distribution among the divisions of the country and the states, but also among the cities, towns, villages and rural areas. This is all given in the report in detail. The analysis of the material yields a number of interesting facts. We note that the Jews have now spread to every place of 25,000 or over and that there are residents of Jewish faith in nearly 10,000 cities, towns, villages and rural areas in the country. As regards density, the records show that the Jews form 11.11 per cent of the total

population in cities of the class of 100,000 population or over, while in the class of cities of the size of 10,000 to 25,000 they constitute 3.11 per cent, and only 1.61 per cent in the class of 25,000 to 100,000 population.



ALMA MATER or *The Future of Oxford and Cambridge. To-day and To-morrow Series.*
By Julian Hall. E. P. Dutton and Co.

\$1.00 4½ x 6; 96 New York

In this number of the To-day and To-morrow series a newly fledged Oxonian tells what the English undergraduate is thinking. Most, it seems, refuse to believe that life is real, life is earnest, but there is a more serious minded minority who have faith in Mr. Wells' Open Conspiracy and who by the next generation will have leavened the whole lump. "The new education will be inspired by a conscious purpose, to which each step will contribute. It will fashion your outlook in accordance with a definite plan. The whole idea of the conspiracy takes rise from a set of historical, biological and sociological realizations; and at school these will be summarized for you as they exist up to date." The prospect seems almost as alluring as the Soviet régime or one of Mr. Ford's factories. We submit also that a sometime scholar of Balliol should know that the word *data* is a plural form.



THE STORY OF RELIGION *as Told in the Lives of Its Leaders.*

By Charles F. Potter.

Simon and Schuster, Inc.

\$5.00 6¼ x 9¼; xx + 627 New York

More than two centuries ago Swift noted that "to enter the Palace of Learning at the *great Gate*, requires an Expende

of Time and Forms; therefore Men of much Haste and little Ceremony, are content to get in by the *Back-Door*." If this was true in the spacious Eighteenth Century, it is doubly true in these bustling days. Outlines of history, of science, of art, of most other mental disciplines, increase and multiply. In the field of religion we have already had Lewis Browne's excellent *This Believing World*. And now Dr. Charles Francis Potter gives us a history of religion in the form of vivacious and sometimes rather flippant sketches of the lives of Akhenaten, Moses, Zoroaster, Jeremiah, Buddha, Confucius, Jesus, Paul, Augustine, Patrick, Muhammad, Aquinas, Nanak, the founder of the Sikhs, Luther, Nicon, the Russian reformer, Wesley, and a group of American religious leaders ranging from Roger Williams to Mary Baker Eddy. In the chapter on Jesus we find no mention of the conclusion of Drews, Couchoud, J. M. Robertson and others that Jesus was a wholly mythical character. Dr. Potter's treatment is essentially Renan watered down and jazzed up.



THE ART OF LIFE. *From the Works of Havelock Ellis.*

Selected and arranged by Mrs. S. Herbert.
Houghton Mifflin Co.

\$2.00 4 $\frac{3}{4}$ x 7 $\frac{1}{2}$; 149 Boston

As reading matter, these "precious" selections, chosen from a group of the famous Englishman's writings, are tantalizing and unsatisfactory. In glancing through the book one continually has the desire to see each or at least many of the selections exhibited in their native background rather than grouped with numerous other selections. Perhaps, however, the chief rôle of the book is to give a general survey of the comprehensive mind of this wise observer of human thought and

action. His philosophy is summed up in one sentence. "All the art of living lies in a fine mingling of letting go and holding in." Again and again, throughout the anthology, under the different headings "love," "morality," "religion," and "philosophy" we find this *motif* appearing and reappearing in one form or another.



HIBERNIA or *The Future of Ireland. To-day and To-morrow Series.*

By Bolton C. Waller. E. P. Dutton and Co.
\$1.00 4 $\frac{1}{2}$ x 6; 96 New York

Mr. Waller points out that the two aspirations, Freedom and Unity, involved in the phrase "Ireland a Nation," are by no means necessarily connected, that there is much more likelihood of achieving unity under the present status of substantial self-government than under complete independence. His record of the accomplishments of the new régime in agriculture and hydro-electric development is encouraging. While solicitous for the preservation of an Irish national culture, he is sceptical of the program of the extreme Gaelicists. His remark on Protection is as germane on this side of the water as on the other: "To tax the general body of citizens in order to provide secure and comfortable incomes for inefficient manufacturers of unessential commodities is the worst possible national economy."



REPORT ON THE STATISTICAL ANALYSIS OF THE MEDICAL EXAMINATIONS (1924-25 TO 1926-27) OF STUDENTS OF THE MYSORE UNIVERSITY.

By K. B. Madhava. University of Mysore
6 x 9 $\frac{1}{8}$; 80 (paper) Mysore, India

Measurements on 2,740 students at the two centers of Mysore University (Mysore

and Bangalore) covering a period of three years, constitute the basis of this report. In the group there are thirty-eight women. Records of body size and dimension, visual and other defects, diseases, etc., were made. In general the data of the two centers are analyzed separately. Also in some instances the Brahman and Non-Brahman records are segregated. One of the interesting results of such analysis is found in the comparison of body weight of the two sects, where there is indication that the "Non-Brahmans are as a rule heavier than their Brahman colleagues by above 4 to 7.5 pounds." Regarding the effect of university education in gain and loss in body weight the results, while not conclusive, indicate the importance of collecting extensive and reliable data on this point. The report closes with a brief historical account of medical inspection of students in various countries and cities.



AMONG THE FOREST DWARFS OF MALAYA.

By Paul Schebesta. Translated by Arthur Chambers. Hutchinson and Co., Ltd.
21 shillings 5 $\frac{1}{8}$ x 9; 288 London

An interesting account of a stay of nearly two years among the inland forest dwelling dwarfs of Malaya, generally called Semang, or Orang-Utan (meaning literally "forest dwellers"). The book is abundantly and well illustrated with photographs. It contains a wealth of ethnological information. The Semang are nomads, and extremely shy. To accomplish anything in the way of investigation of them it is necessary to live with them and move with them. In tropical forests with an excessive rainfall this is not the most comfortable enterprise conceivable for a European. The author notes that the Semang are dying out.

A great dearth of women is making itself felt in their ranks and the vices of the cultured races are gaining a hold on them, especially opium-smoking. Syphilis is, as far as I know, unknown among them. European civilisation is digging the grave of the dwarfs of Malaya as it presses further into the interior, thrusting the Malays before it and crowding the nomadic Semang into an area too confined for them where they are being economically smothered.

There is a good map, and an index.



ZYGOURIES. *A Prehistoric Settlement in the Valley of Cleonae. Published for the American School of Classical Studies at Athens.*

By Carl W. Blegen.

Harvard University Press
Cambridge

\$15.00

9 x 12; xviii + 227 + 22 plates

A magnificently produced monograph giving the results of excavations of a prehistoric site, dating from the Bronze Age. The prehistoric deposit could be clearly divided into three main layers, Early, Middle and Late Helladic. The finds are discussed under four main heads: Architecture; tombs; pottery; miscellaneous objects. The book is beautifully and extensively illustrated, the colored plates of pottery being especially fine.



THE PRIVATE CORRESPONDENCE OF NICOLÒ MACHIAVELLI.

By Orestes Ferrara.

The Johns Hopkins Press

\$2.25 6 x 9; xii + 130 Baltimore

Started by a systematic campaign of defamation and misrepresentation during his life-time, there has grown up during the centuries a legend about Machiavelli, which recent research is showing to have been almost wholly at variance with reality. Doctor Ferrara, a distinguished student of Machiavelli, in this readable

book makes a further contribution towards dispelling this myth. In truth Machiavelli was a kindly, shy man of high intelligence who somewhat naïvely attempted to look at human behavior realistically. He died a disappointed and puzzled man. We recommend this book.



METANTHROPOS or *The Body of the Future. To-day and To-morrow Series.*
By Ronald Campbell MacFie.

E. P. Dutton and Co.

\$1.00 4 $\frac{1}{8}$ x 6; 96 New York

The author does not think that evolution will change the human body much in the future, except perhaps as regards the neopallium, and while there are signs of deterioration in the race, on the whole the future looks good. It is certain that matrimonial selection will produce a healthy race and science will find cures or prophylactics for all diseases. This thesis is set out as a running commentary on the views of biological and anthropological authorities. We hope that the writer has looked more carefully into the views he quoted than he has into the spelling of their authors' names. We find, among others, such aberrations as Thomas Haxley, Smith Elliot, J. A. Thompson, Millgan (the physicist), as well as the Piltsdown man.



EXCAVATIONS IN OLYNTHUS. *Part I. The Neolithic Settlement. The Johns Hopkins University Studies in Archaeology No. 6.*

By George E. Mylonas.

The Johns Hopkins Press

\$7.50 7 $\frac{1}{4}$ x 10 $\frac{3}{4}$; xvii + 108 Baltimore

A detailed and beautifully illustrated account of the neolithic relics found in connection with the excavations at a site

which has proved to be that of classical Olynthus, near a small village Myriophyto in Macedonia. The excavations have been made under the direction of Prof. David M. Robinson. The neolithic settlement flourished about 3000 B.C. Many of the finds are unique, including the first neolithic kiln to be discovered in Greek lands, the earliest zoomorphic vases, and the earliest religious idols so far discovered in Macedonia. Successive chapters deal with the site; architectural remains; pottery; figurines; celts; smaller finds; and affinities with other prehistoric sites. A valuable contribution to prehistory.



YOUR FAMILY TREE.

By David Starr Jordan and Sarah L. Kimball.

D. Appleton and Co.

\$3.00 5 x 8; xi + 346 New York

This book is a pious monument to the fecundity of Lady Isabel de Vermandois and her two assistants, Robert de Beaumont, Count of Meullent, and William de Warren, Earl of Warren. All of us, or at least a lot of us, owe our existence here and now, according to the venerable and beloved author of this book, to Isabel's assiduity in what may be hoped—indeed believed—to have been a pleasant, and, for posterity, profitable task. Reginald, the Office Boy, has presented a difficult problem since this book fell into his clutches. He struts about the place like a pouter pigeon, because he says he is related to Aeneas, Wotan, and Calvis Coolidge, and can prove it by the book.



FOODS OF THE FOREIGN-BORN in Relation to Health.

By Bertha M. Wood. M. Barrows and Co.

\$1.25 4 $\frac{1}{2}$ x 7 $\frac{1}{2}$; ix + 110 Boston

This little book, a second edition, will be found extremely useful by dietitians and nurses working among our foreign populations. It will be of interest also to those who like to experiment with foreign cookery. Recipes of many palatable but fairly inexpensive dishes of different nationalities, largely European and Near East, are given. In an appendix there are analyses of the food values of the various recipes.



ACROSS THE GULF. *A Narration of a Short Journey through Parts of Yucatan with a Brief Account of the Ancient Maya Civilization.*

By Ralph F. Seymour.

The Alderbrink Press.

\$7.00 7½ x 10½; 63 Chicago

A beautifully printed and illustrated book, issued in limited edition. It is a delightful account of a pleasure trip to Yucatan. The point of view is that of an artist, and the discussion of the Maya remains from that angle is illuminating. The woodcuts by the author are superb.



TRENDS IN PROTESTANT GIVING. *A Study of Church Finance in the United States.*

By Charles H. Fabs.

Institute of Social and Religious Research

75 cents 6 x 9; 67 (paper) New York

A study of the finances of the leading Protestant churches in the United States shows that the increase in gifts per capita failed to compensate for the decrease in value of the dollar during the war and in the case of gifts for congregational expenses through 1922. Since then they have more than compensated. The proportion of these gifts devoted to benevolences rose from 21 per cent in 1913 to 35

per cent in 1920 and then fell back to 22 per cent in 1927. The marked increase in indebtedness on church and parsonage property and the lessened appeal of the centralized efficiency systems installed after the war, as compared with the older, less organized, but more personal methods, are suggested as possible causes of this weariness in good works.



RACE CROSSING IN JAMAICA. *Carnegie Institution of Washington Publication No. 395 (Paper No. 36 of the Department of Genetics).*

By C. B. Davenport and Morris Steggerda (In collaboration with F. G. Benedict, Lawrence H. Snyder, Arnold Gesell, Inez Dunkelberger Steggerda and many residents of the colony of Jamaica).

Carnegie Institution of Washington

\$7.00 (paper)

Washington

\$8.00 (cloth)

6½ x 10; ix + 512

An anthropometric, physiological, psychological, developmental and eugenic study of Jamaican whites, blacks, and hybrids. The blacks showed themselves superior to the whites in tests of musical capacity, but inferior in operations which require good judgment. The greater likeness of the hybrids to the blacks than to the whites is explained as due to back crossing with the blacks rather than to dominance of the Negro characters.



PROCEEDINGS FIRST COLLOQUIUM ON PERSONALITY INVESTIGATION.

Held Under the Auspices of the American Psychiatric Association. Committee on Relations with the Social Sciences. December 1-2, 1928.

Lord Baltimore Press

60 cents (paper) 5½ x 9½; 102 Baltimore
\$1.00 (Cloth)

The record of a get-together meeting between a group of psychiatrists and a group of social scientists. The reader is left at the end wondering with little Peterkin what good came of it at last, whether either side attained a better grasp of the other's point of view than at the beginning.



DER NORDISCHE MENSCH. *Die Merkmale der nordischen Rasse mit besonderer Berücksichtigung der rassischen Verhältnisse Norwegens.*

By Halvdan Bryn. J. F. Lehmanns Verlag
9 marks (paper) München
11 marks (cloth) 6 x 9; 166

An excellent treatise on the physical characteristics and ethnology of Nordic man, with the Norwegian as a particular example treated in detail, written by one of the most distinguished Norwegian anthropologists. The book is attractively printed and abundantly illustrated. There is a bibliography of 112 titles, and a good index.



AGRICULTURAL EDUCATION IN THE UNITED STATES.

By Whitney H. Shepardson.
The Macmillan Co.
\$1.50 $4\frac{7}{8} \times 8\frac{3}{8}$; viii + 132 New York

Within its limitations of space this book is perhaps the best statement that has ever been made of the history, present status, opportunities and weaknesses of agricultural education and research in the United States. It was prepared as a report for the General Education Board, while the author was in the employ of that body, but we are told that now the General Education Board does not endorse its substance. The author was returned to business life "after a strange and stimulating interlude."

REPORT OF WAGE AND PERSONNEL SURVEY. *Field Survey Division, Personnel Classification Board. 70th Congress, 2d Session. House Document No. 602.*

U. S. Government Printing Office
60 cents $5\frac{3}{4} \times 9\frac{1}{8}$; v + 511 Washington

A detailed study of the problem of the salaries and classification of government employees. Extensive data on salaries of comparable workers outside the government are presented in detail. The volume will be useful to the student of human biology for reference purposes.



HEREDITY AND PARENTHOOD.

By Samuel C. Schmucker. The Macmillan Co.
\$2.50 $5\frac{1}{2} \times 8$; x + 322 New York

An interesting, well written book on the biological foundations of eugenics, intended for the reader without training in biology. It is one of the best books of the sort we have seen.



RACE AND POPULATION PROBLEMS.

By Hannibal G. Duncan.
Longmans, Green and Co.
\$2.50 $5\frac{1}{4} \times 8$; xv + 424 New York

In this book the author "has endeavored to combine the old type of textbook with the more recent type of a book of readings, and has striven to refrain from injecting his own conclusions." If the result sounds rather like the *Literary Digest* it at least proves to the student that Doctors—of Philosophy as well as of Medicine—disagree.



VULCAN or *The Future of Labour. To-day and To-morrow Series.*

By Cecil Chisholm. E. P. Dutton and Co.
\$1.00 $4\frac{1}{8} \times 6$; 95 New York

As a result of future improvements in management and machines the worker—

as soon as the slight detail of the utilization of atomic energy is solved—will, after his one day a week of labor, be able to step into his airplane for a six day jaunt on the continent. There is no indication in the book that Mr. Chisholm has ever heard of Malthus.



HEREDITY AND HUMAN PROBLEMS.

A Series of Eight Radio Talks. (With Select Bibliography). Radio Publication No. 50, University of Pittsburgh.

By P. W. Whiting. University of Pittsburgh
60 cents $5\frac{1}{8} \times 8\frac{1}{2}$; 87 (paper) Pittsburgh

In this group of necessarily popular lectures the author has succeeded in giving to the layman a very fair view of some of the present day problems of heredity and their importance in human relations.



ZOOLOGY

EOÖRNIS PTEROVELOX GOBIENSIS.

By Augustus C. Fotheringham.

The Buigleigh Press

75 cents $7\frac{1}{2} \times 10$; 34 (paper) London

(Copies may be obtained from Dr.

Lester W. Sharp, N. Y. State

College of Agriculture, Cornell

Univ., Ithaca, N. Y.)

This monograph in a first edition of 500 copies reports the results of the British Museum's expedition to the Gobi desert to secure definitive information regarding the creature designated by Linnaeus *Micropteron asiatica*, renamed by the authorities *Eoörn is pterovelo x gobiensis* and popularly known as the "woofen poof." This rare bird was known to prehistory and antiquity, reproductions of it being found on the walls of the Crô Magnon caves, in an amulet of King Tut-an-kh-amen and being mentioned by the Roman historian Eutro-

pius as well as by Marco Polo. At present it is found only in a circumscribed region of the Gobi desert where the expedition accordingly went to make its observations.

The investigation covered the biology of the animal in a broad sense; general morphology, habits, life history, anatomy, embryology, physiology, pathology, psychology, taxonomy, phylogeny, and sociology are reviewed in separate sections. Some, if not all, of the findings are remarkable. We have not the space to present them adequately, but a few of the more startling may be mentioned.

The eggs, which have a flexible, rubber-like shell, hatch out twins, a male and a female comprising each batch. These same individuals later mate, the animal being monogamous, although careful cytological studies show that the eggs develop parthenogenetically. The food consists almost exclusively of the sand-flea *Fugifex pugens* which the bird consumes in large numbers, a contemporary substitute for the now extinct Crô Magnon worm. The flight is extremely rapid, reaching as high as 600 km. per hour, and the vibrations of the wings emit a characteristic note pitched usually at G below middle C. Of interest in this connection is the discovery that the albino variety is soundless, owing probably to an alternation in the use of each wing, one neutralizing the sound of the other. Psychological studies prove that *a priori* and *a posteriori* reasoning are equally potential. When placed exactly between two piles of sandfleas, the bird languished to a death of starvation, unable to decide from which pile to feed. Ordinarily it dies from 7 to 35 years of age from deliquescence of the lumbar ganglion, resulting in a form of avian Bright's disease. The book is amply illustrated with photographs and diagrams, and written in a properly reserved but extremely entertaining style.

In view of the scholarly care with which the work is otherwise constructed we can excuse the typographical error in the spelling of the publishing house from which it was issued. Obviously it should read D'm Bigleigh Press.



CATALOGUE OF THE MADREPORARIAN CORALS IN THE BRITISH MUSEUM (NATURAL HISTORY). Vol. VII. *A Monograph of the Recent Meandroid Astraida.*

By George Matthai.

The British Museum (Natural History)

£ 3, 3s.

London

9½ x 12¼; v + 288 + 72 plates

This magnificent monograph completes an investigation begun in 1914 by Prof. J. Stanley Gardiner.

An attempt is made at a revision of the Meandroid Astræid corals based on a comparative study of their hard and soft parts. But of the twenty-eight genera and sixty species described, the soft parts of only fourteen genera and twenty-three species were available for study. The structure of the polyps of eight genera and sixteen species is described for the first time. Three of the genera, viz. *Isophyllastrea* gen. nov., *Protomussa* gen. nov. and *Caulastrea* Dana, do not belong to the Meandroid group as they have distinct corallites. In addition to these, notes on *Tridacophyllia manicina* Dana, and on three doubtful species, viz. *Mussa lacinians* M. Ed. & H., *Favia astræiformis* (M. Ed. & H.) and *Favia spongiosa* (Dana) are also included.

The plates accompanying this Monograph contain photographs of some of Dana's types taken while I was working in the U. S. National Museum, Washington, of the existing types of Lamarck, Milne Edwards and Haime, Ehrenberg and Esper, and some of Rehberg's, as well as of a specimen believed to be Linnæus' type of *Madrepore areolata* in the collection of the Linnean Society of London. Six figures cited by Linnæus under *Madrepore labyrinthiformis*, *M. areolata* and *meandrites*, and one on which P. L. S. Müller based *Madrepore amaranthus* (1775), are also reproduced. The remainder of the photographs are of representative specimens in the British Museum (Natural History).

The heliotype plates are superb.

EXPERIMENTAL-ZOOLOGIE. VI BAND: ZOONOMIE.

Eine Zusammenfassung der durch Versuche ermittelten Gesetzmässigkeiten tierischer Formbildung (experimentelle, theoretische und literarische Übersicht bis einschliesslich 1928).

By Hans Przibram. Franz Deuticke
40 marks Vienna

7 x 10¼; viii + 431 + 16 plates
(paper)

Of this sixth volume of Prof. Przibram's review of the results of experimental zoology, 140 pages are devoted to bibliography. What would be text figures (line cuts) in normal book producing practice, are relegated to the back of the book as plates. The arrangement of the material is taxonomic in the major portion of the text. Altogether it seems to us that it would have been possible to make a more interesting and readable book than this is, considering the enormous amount of labor which went into its preparation.



FIELD BOOK OF MARINE FISHES OF THE ATLANTIC COAST FROM LABRADOR TO TEXAS. *Being a Short Description of Their Characteristics and Habits with Keys for Their Identification.*

By Charles M. Breder, Jr.

G. P. Putnam's Sons

\$5.00 4 x 6¼; 332 New York

This excellent "handy volume," the first of its kind to appear, will be found extremely useful by both naturalist and angler. While the material has been culled largely from technical books and papers, the author has also contributed much new material from his own observations and wide experience. The book opens with brief introductory chapters on the identification, range, and manner of life of marine fishes. The descriptions of general habits, range and prominent features of each species are given in great

detail, while the identification of these is greatly facilitated by the excellent colored and black and white plates, as well as by the innumerable line drawings. At the end of the volume there is an all too brief bibliography, a glossary of technical terms, and an index.



A MANUAL OF EXTERNAL PARASITES.

By Henry E. Ewing. Charles C. Thomas
\$4.50 Springfield, Ill.

$5\frac{7}{8} \times 8\frac{3}{4}$; xiv + 225

This volume deals with the external anatomy, life history and natural relationships of the five major groups of ectoparasites: the mites, the ticks, the biting lice, the sucking lice, and the fleas. Keys are given to most of the known genera. There are numerous excellent illustrations, which will greatly assist in the identification of the different forms, and useful suggestions for their control. The book is well documented and will be found valuable as a reference book by those whose line of work requires a knowledge of parasitology, as well as by the student of general biology and entomology.



EXPERIMENTS IN MARKING YOUNG CHINOOK SALMON ON THE COLUMBIA RIVER, 1916 TO 1927. Bureau of Fisheries Document No. 1047.

By Willis H. Rich and Harlan B. Holmes.

U. S. Government Printing Office

40 cents

Washington

$7\frac{1}{2} \times 11$; 215-264 + 21 plates (paper)

The results of these experiments, covering a period of eleven years, seem to give conclusive evidence of the "homing" instinct of chinook salmon. None of the tagged fish, liberated in the Columbia

River and wandering as far afield as the waters of Southern Alaska, have been found in any other river stream than in the Columbia. Normally the fish tend predominately to return to spawn in the tributary in which they spent their early lives. The experiments indicate that the best plan in stocking waters is to plant each stream with eggs native to that stream. Other facts reported on in the paper are the "percentage of return," "success of long and short periods of rearing," "interpretation of scales," "time of entering fresh water," and "age at maturity." The text includes numerous tables concerning the results of the thirteen series of experiments carried on at different hatcheries on the Columbia River. Photographic plates show the system of scale markings, etc. while there is a bibliography of sixteen titles.



MANUAL OF THE VERTEBRATE ANIMALS OF THE NORTHEASTERN UNITED STATES INCLUSIVE OF MARINE SPECIES. Thirteenth Edition.

By David Starr Jordan (with an Introduction by Barton W. Evermann).

World Book Company

\$4.00 $5\frac{3}{8} \times 9$; xxxi + 446 Yonkers, N. Y.

A revised edition of the vertebrate manual which has been standard for fifty years. The district covered is, approximately, the northeastern United States and southern Canada, extending from Labrador westward to and including Manitoba and North Dakota, and southward to and including North Carolina and Kansas. The resident shore fishes of the region are included, but for the most part not the strays from the Gulf Stream or the fishes of the Deep Seas. The birds which are chance wanderers from Europe or the West Indies are also omitted or, at the most, merely mentioned.

THE PLANT LICE OR APHIDAE OF GREAT BRITAIN. Vol. III.

By Fred V. Theobald. Headley Brothers
30 shillings London

5½ x 9; vi + 364 (paper)

With the issuance of this volume the description of the British aphides, so far as at present known, is completed. The investigator has maintained the same standard of excellence exhibited by the previous volumes, both of which have been mentioned earlier in these columns. The third section opens with the subtribe Chaitophorina. Students of agriculture, horticulture and forestry will find this completed work an invaluable addition to their list of reference books.



OUTLINES OF GENERAL ZOÖLOGY.

By Horatio H. Newman. The Macmillan Co.
\$3.50 5½ x 8½; xxii + 541 New York

A revised second edition of this admirable text. The changes from the first are considerable. Material has been added to make it adequate for a year course, and the last part on general principles of zoölogy redone under the title "Dynamic Aspects of Zoölogy," giving it more of a physiological content than it had in the former arrangement.



COREGONID FISHES OF THE GREAT LAKES. Bureau of Fisheries Document No. 1048.

By Walter Koelz.

U. S. Government Printing Office
\$1.10 7½ x 11; 346 (paper) Washington

This excellent monograph contains the report of an extensive study of the coregonid fishes from an economic as well as a scientific viewpoint. The author deals with the distribution of these forms in the various waters of the Great Lakes

region, their natural history and the conditions under which they live, their origin and evolution, and their relationships with one another and with the coregonids of other parts of America, as well as Asia and Europe. The paper contains 101 tables, a number of figures, a lengthy bibliography and distribution maps of the various lakes studied.



CAPITA ZOOLOGICA. II. aft. 7. *Freilebende Marine Nematoden von der Nordwest-Kueste Frankreichs (Trébeurden: Côtes du Nord).*

By Hans A. Kreis.

Martinus Nijhoff

10 guilder

The Hague

9½ x 13; 98 + 8 plates (paper)

This monograph on the free-living marine nematodes of the coast of Brittany includes interesting sections on morphology and biology and ecology. The collection was rather rich. It included 485 individuals included in 34 genera with 46 species. It is well illustrated, indexed, and documented. It does credit to the series in which it is included.



TYPICAL FLIES. *A Photographic Atlas of Diptera. Series III.*

By E. K. Pearce.

Cambridge University Press

10 shillings net

London

7 x 10½; xiv + 64

This little volume, the third in the series, presents us with a group of remarkably fine photographs of many flies of diverse groups of British Diptera. The usefulness of this volume to the student is enhanced by the brief notes on size, coloring, general appearance and habits accompanying each illustration, the preface giving full information for collecting and preserving specimens, a bibliography, and an index.

A new edition of the text which is the pedagogical standard for introducing the American student to the science of embryology.



PHYSIOLOGY AND PATHOLOGY

THE ANNALS OF THE PICKETT-THOMSON RESEARCH LABORATORY. *Volume IV, Part II. The Pathogenic Streptococci. An Historical Survey of Their rôle in Human and Animal Disease.*
The Williams & Wilkins Co.

Baltimore

\$10 per volume (Parts I and II)

8½ x 11½; viii + 243 (paper)

The issue, containing the second group of studies on pathogenic streptococci, completes Volume IV of the Annals from the Pickett-Thomson Research Laboratory. Reviews of two previous volumes on streptococci have appeared earlier in these columns. In the present number the first two monographs (V and VI in the completed volume) on "the rôle of the streptococci in acute and subacute suppurative arthritis" and "the rôle of the streptococci in chronic arthritis," are by the co-workers David and Robert Thomson. The third and last monograph (VII) is by H. Warren Crowe on "Rose-now's hypothesis of elective localization." It has been the aim of these workers to bring together a more or less complete résumé of researches in this field, as well as to present important views and theories held by various clinicians. The present work includes also reports on a study of "the experimental production of foci of infection in rabbits and its bearing on osteo-arthritis," by H. Warren Crowe and "a simple and rapid test for the differentiation of streptococci," by David

Thomson. Each monograph includes extensive reference lists. There are excellent photographic plates belonging to Monograph VI. Detailed author and subject indices for Volume IV complete the work. Volume V, to be issued at a later date, will contain studies on the rôle of the streptococci in oral and dental sepsis and tonsillitis.



THE GENUINE WORKS OF HIPPOCRATES. *Translated from the Greek with a Preliminary Discourse and Annotations. Two volumes in one.*

By Francis Adams. William Wood and Co.
\$6.00 New York

6 x 9½; Vol. I, vi + 390
II, 366

It is now eighty years since the good physician of Banchory published his translation of the Hippocratic *corpus*, of which this is a new edition. The translation is excellent, but progress in medical knowledge has rendered obsolete many passages in the introduction and notes.

The astonishing modernity of the ancient Greeks is strikingly shown in the passage on the Macrocephali in the *Airs, Waters and Places*:

There is no other race of men which have heads in the least resembling theirs. At first, usage was the principal cause of the length of their head, but now nature coöperates with usage. They think those the most noble who have the longest heads. It is thus with regard to the usage: immediately after the child is born, and while its head is still tender, they fashion it with their hands, and constrain it to assume a lengthened shape by applying bandages and other suitable contrivances whereby the spherical form of the head is destroyed, and it is made to increase in length. Thus, at first, usage operated, so that this constitution was the result of force: but, in the course of time, it was formed naturally; so that usage had nothing to do with it; for the semen comes from all parts of the body, sound from the sound parts, and unhealthy from the unhealthy parts. If, then,

children with bald heads are born to parents with bald heads; and children with blue eyes to parents who have blue eyes; and if the children of parents having distorted eyes squint also for the most part; and if the same may be said of other forms of the body, what is to prevent it from happening that a child with a long head should be produced by a parent having a long head?

If this is not an anticipation both of Lamarckianism and of Darwin's hypothesis of pangenesis we are ready to eat our hat.



MEDICINE. *Its Contribution to Civilization.*
By Edward B. Vedder.

The Williams & Wilkins Co.

\$5.00 6½ x 9½; ix + 398 Baltimore

A well written account for the general reader of the present state of medicine and especially of preventive medicine. Colonel Vedder begins with the recognition that in many diseases, such as tuberculosis and meningitis, not all persons exposed to the causative organism contract the disease, that both constitutional diathesis and environmental factors are predisposing causes. He then treats the infectious diseases, nutrition and nutritional diseases, diseases of the glands of internal secretion, degenerative diseases, the conquest of disease, the cancer problem, and modern preventive medicine. Unlike Hoffman he concludes that the increase in the published crude death rates from cancer is due to improved diagnosis and to changes in the age distribution of the population.



DEVILS, DRUGS, AND DOCTORS. *The Story of the Science of Healing from Medicine-Man to Doctor.*

By Howard W. Haggard. *Harper and Bros.*

\$5.00 6 x 9½; xxii + 405 New York

The great advances that have occurred

in medical practice are here thrown into bold relief by a method of hyperbolic contrast. The past is represented by filth, ignorance, bigotry, cruelty and suffering, relieved by an occasional generous and progressive individual. The present, except for the osteopaths *et al.*, is enlightenment and sanitation. This black and white picture of medical history fails to give a well balanced view of the gradual growth of medical knowledge and the important place that general science has had in it, but what it lacks of even objectivity it gains in high dramatic interest. The matters dealt with are chosen for their great human interest, childbirth, anesthesia, surgery, plague, etc., and the individual events for their melodrama and picturesqueness. The whole makes an exciting story, and it is superbly illustrated by reproductions from contemporary artists and cartoonists. It is well done as a piece of bookmaking and contains an index.



THE MINIMUM PROTEIN REQUIREMENTS OF CATTLE. *Report of Committee on Animal Nutrition. Bulletin of the National Research Council No. 67.*

By H. H. Mitchell.

National Research Council

\$1.00 6½ x 9½; 84 (paper) Washington

This report gives the results of applying a method of measuring protein requirements, proposed by the Sub-Committee on Animal Nutrition, to experimental data on beef and dairy cattle already available. Concerning the results obtained, the author states that they are

not to be compared with values already current in the literature. Heretofore, protein requirements have been expressed in two ways, either in terms of digestible crude protein or in terms of digestible true protein. Statements thus expressed are ambiguous, since they are not related to protein of any definite or known biological value. In this report, protein

requirements are expressed in terms of animal expenditures or storages of nitrogen, converted for convenience into conventional protein ($N \times 6.25$). They may be considered as representing the requirements for digestible crude protein possessing a biological value of 100. They are thus definite in their significance, minimal in the truest sense of the word, and adaptable to any protein mixture the biological value of which may be satisfactorily estimated.

There are 32 tables in the text and a bibliography of 99 titles.



REPORTS SUBMITTED BY THE RADIOLOGICAL SUB-COMMISSION. *League of Nations, Health Organisation, Cancer Commission. Publication III. Health 1929. III. s. Official No. C. H. 788.*

League of Nations

\$1.50 7½ x 10; 82 (paper) *Geneva*

Contains the rules adopted for obtaining full and comparable statistics in regard to incidence and treatment of utero-vaginal carcinoma and several special reports of particular experience with radiotherapy as follows: Report on the technique and results of the treatment of cancer of the uterine cervix at the Radiumhemmet at Stockholm, by J. Heyman; Report on the technique and results of the radiotherapeutic treatment of cancer of the uterine cervix at the Radiological Section of the University Gynaecological Clinic at Munich, by F. Voltz; Report on radiotherapy in the treatment of epitheliomata of the uterine cervix at the Radium Institute at Paris, by A. Lacassagne.



THE HUMAN MECHANISM. *Its Physiology and Hygiene and the Sanitation of its Surroundings.*

By Theodore Hough and William T. Sedgwick. Second revised edition by J. A. Waddell.

Ginn and Co.

\$3.00

5 x 7½; 691

Boston

A text written for the very ignorant public and saturated with the noble spirit of uplift. Tobacco, it is stated somewhat elaborately, is taken in three forms: (1) smoking, (2) snuffing, (3) chewing. All are bad to different degrees and lead to

(1) disorders of the digestive system or capricious appetite frequently needing coaxing by tonics; (2) enlargement of the heart and irregularity in its action, called tobacco heart, in which changes in position and emotions produce a violent increase in rate; and (3) impairment in nervous activity. . . . It can hardly be doubted that many a young man has failed to make the most out of life because this habit contracted in youth has brought about a weakening of the foundations upon which he subsequently had to build, and, in consequence, he became stunted mentally and physically.

Some states, it is mentioned suggestively, prohibit its sale by law.



COMMON COLDS. *Causes and Preventive Measures.*

By Leonard Hill and Mark Clement.

William Heinemann, Ltd.

7 s. 6 d. net

London

5½ x 8½; 126

An excellent treatise on common colds, giving not only a great deal of information about the conditions under which the cold germ flourishes and the more serious disabilities which so frequently follow an infection, but some very sound advice on the prevention of colds, particularly as regards diet, exercise, clothes, and rest. In brief, the warning is that he who would protect himself from colds must guard against loss of tone in his protective structure. If these structures—the skin (which is rated first in importance) and the mucous membranes of nose and throat—have the ability to react quickly to changes in temperature and humidity, then the ever present cold germ has little opportunity to get in its devastating work.

ARE THE GREAT AMERICAN SALT, SUGAR, WHITE FLOUR, HOT DRINKS, VINEGAR, HEN EGG AND TOBACCO DEBAUCHES PARTIALLY RESPONSIBLE FOR CANCER, INFANTILE PARALYSIS, INFLUENZA, CONSUMPTION, WHOOPING COUGH AND THE ALARMING INCREASE IN HEART FAILURE?

By H. H. Harwood. H. H. Harwood

For price inquire of author. Richmond, Va.

6 x 9; 208 (paper)

This curious volume consists very largely of quotations from the writings of well-known investigators, physicians, surgeons, health officers, and uplifters, interspersed with the author's loosely drawn conclusions that certain articles of diet and tobacco are in part responsible for certain diseases. We offer for the reader's consideration a sample of the result of his mental gyrations: "So, in studying Infantile Paralysis, only a one-tenth-educated physician could imaginably leave tobacco-smoke off his list of probably contributing causes."



MORPHEUS or *The Future of Sleep. Today and To-morrow Series.*

By D. F. Fraser-Harris.

E. P. Dutton and Co.

\$1.00 4½ x 6; 94 New York

Four-fifths of this essay deals with the "today" and one-fifth with the "to-morrow" of sleep. The first reviews the little that is known about its physiology and gives some common sense advice regarding its hygiene. The chapter on dreams could be a great deal more interesting than it is. About the only suggestion for improving sleep in the future is that anyone shouting, singing, or whistling after eleven P.M. be subject to arrest. Nothing is advanced respecting yowling cats or crying babies.

WORK OF THE CANCER COMMISSION. *League of Nations Health Organisation. (Exposé by Sir George Buchanan to the Health Committee. Extract for the provisional minutes C. H. /14th Session/P. V. 7, May 7th, 1929). Official No. C. H. 800.*

League of Nations

Not on sale

Geneva

8 x 13; 8 mimeographed pages (paper)

Minutes of the oral report of the President of the Cancer Commission of the Health Section of the League of Nations regarding its work. The chief accomplishment of the Commission is the report on Radiotherapy noticed elsewhere in this number.



DIE HORMONE. *Ihre Physiologie und Pharmakologie. Vol. 1. Keimdrüsen, Hypophyse, Nebennieren.*

By Paul Trendelenburg. Julius Springer

28 marks (paper)

Berlin

29.60 marks (cloth)

6¼ x 9½; xi + 351

The first of a two volume work reviewing the literature of the hormones of the gonads, the hypophysis and the suprarenal. It is very thoroughly done, and carries the references up to the end of 1928. There is a detailed subject index. The book is a useful contribution to the reference literature of a lively field of biology.



ESSENTIALS OF GENERAL PHYSIOLOGY.

By Eric Ponder. Longmans, Green and Co.

\$3.60 5½ x 8; vii + 497 New York

An introductory text covering the ground broken by Bayliss' classic, *Principles of General Physiology*. It does not exhibit anything like the originality or fine literary quality of the latter.

YOUTHFUL OLD AGE. *How to Keep Young.*

By Walter M. Gallichan.

The Macmillan Co.

\$2.50 5½ x 7½; xii + 236 New York

Pleasant, if rambling, discourse about personal hygiene in relation to the problems presented by senescence. The author says that constipation is the disease that ages. Meat he is opposed to.



BODILY CHANGES IN PAIN, HUNGER, FEAR AND RAGE. *An Account of Recent Researches into the Function of Emotional Excitement.*

By Walter B. Cannon. *D. Appleton and Co.*

\$3.00 5½ x 8; xvi + 404 New York

A second edition, which has been thoroughly revised and enlarged to include the results of all of the latest researches in bodily response to emotion.



SUNRAYS AND HEALTH.

By Ronald Millar. *In collaboration with E. E. Free.* *Robert M. McBride and Co.*

\$1.50 5 x 7½; vi + 125 New York

A sound little book, simply and interestingly written for the general public, on the nature and biological properties of ultra-violet light.



BIOCHEMISTRY

DIE FERMENTE UND IHRE WIRKUNGEN. *Vierter Band: Die Technologie der Fermente.*

By Carl Oppenheimer.

Georg Thieme

75 marks (paper)

Leipzig

83 marks (cloth)

7½ x 10½; xvi + 370

Previous issues in the series which com-

prise this treatise on ferments have been noticed in these columns. The present volume constitutes Band IV of the general work and is devoted to the application of enzyme chemistry to industry. It is divided into two main divisions: the first of these is devoted exclusively to fermentation industries and is by Dr. Albert Hesse; the second considers different industries in successive chapters as follows: Ferments in the fat industry, by Dr. Emil Hoyer; Ferments in the milk industry, by Dr. Walter Grimmer; Ferments in the leather industry, by Dr. Otto Gerngross; Ferments in the gelatin and lime industry, by Dr. Otto Gerngross; Ferments of the pharmaceutical industry, by Dr. Peter Bergell and Herbert Carls; Ferments in the malt-extract industry, by Dr. Albert Hesse; Ferments in the textile industry, by Dr. Albert Hesse; and Ferments in the food industry, by Dr. Albert Hesse. A subject index is appended.



ELEKTRIZITÄT UND EIWEISSE, insbesondere des Zellplasmas.

By Hans Pfeiffer.

Theodor Steinkopff

10 marks (paper)

Dresden

10.50 marks (bound)

6 x 8½; xii + 149

The series of which this book is a number attempts to give succinct reviews of the recent work in various branches of scientific research. The period covered is about the last fifteen years, but earlier work is included where it is germane to contemporary problems. The present volume covers the colloid and electrical properties of proteins and leads into a consideration of the play of these in protoplasm. It is well supplied with bibliography and contains an author and subject index that adds greatly to its value as a working reference.

PRACTICAL PLANT BIOCHEMISTRY.

By *Muriel W. Onslow.**Cambridge University Press*12s 6d. $6\frac{1}{2} \times 9\frac{1}{8}$; 206 *London*
\$4.25 (*The Macmillan Co., New York*)

A third edition of this highly successful text. The chapter headings will indicate its scope: Introduction; the colloidal state; plant enzymes; chlorophyll; carbohydrates; the vegetable acids; fats and allied substances; aromatic compounds; proteins and amino-acids; glucosides; plant bases. There are bibliographical references appended to each chapter and a general index at the end.



ELEKTROCHEMIE DER KOLLOIDE.

By *Wolfgang Pauli and Emerich Valkó.**Julius Springer*66 marks (paper) *Vienna*
68 marks (bound) $7 \times 10\frac{1}{4}$; xii + 647

A substantial contribution to the literature of colloids. The foundation of the discussion is laid in an introductory part, reviewing the modern electrolytic theory of solution, and then going on to general and special colloid chemistry. The bibliographic documentation is extensive, and is brought up to date. The book is well indexed and constitutes a valuable reference work.

A CLASSBOOK OF PRACTICAL CHEMISTRY. *First Year.*By *J. Morris.* *Methuen and Co., Ltd.*2 shillings $4\frac{1}{8} \times 6\frac{3}{4}$; viii + 103 *London*

An excellent laboratory guide for a beginner's course in chemistry. While the author has designed it to accompany his *Introduction to Chemistry*, it is so arranged that it can be used in combination with any standard textbook for beginners.

The unique method has been followed of placing on the left hand page the detailed directions for experiments, and on the opposite page the results and conclusions drawn from these experiments. It is intended that the right hand page shall be covered until the student has worked out and written up in his notebook his observations. He then can refer to the correct solution and discover his mistakes, if there are any. Naturally this method works best with those students who are not seeking easy methods to slide through a course.



PRÉCIS DE PHYSICO-CHIMIE BIOLOGIQUE ET MÉDICALE.

By *André Dognon.**Masson et Cie*36 francs $5 \times 7\frac{1}{2}$ inches; viii + 310 *Paris*

This is a condensed summary of the principal data of physical chemistry which are of direct applicability to medicine. The general topics under which the material is divided are: Water and solutions; osmotic pressure; electrolytic ionisation; hydrogen ions; surface phenomena; viscosity; colloidal solutions; general properties of membranes. There is no index, or bibliography. The book is essentially of the quiz-compend type.

HERMES or *The Future of Chemistry. To-day and To-morrow Series.*By *T. W. Jones.**E. P. Dutton and Co.*\$1.00 $4\frac{1}{8} \times 6$; 88 *New York*

In a single chapter unrelieved by humor or imagination the author dilates on the application of chemistry to practical problems in the future. Almost a half concerns fuel; the remainder various other subjects, including food and medicine. The author suggests little more than further developments of what chemistry is already doing.

SHORT LABORATORY COURSE IN GENERAL CHEMISTRY.

By Raymond E. Neal. The Macmillan Co.
\$1.50 4 $\frac{1}{2}$ x 7 $\frac{1}{2}$; viii + 106 New York

Based on Bartlett and Ink's *The Principles of Chemistry and Their Application*. Enough material is provided to fill a two-hour period each week for sixteen weeks.



SEX

THE SEXUAL LIFE OF SAVAGES IN NORTH-WESTERN MELANESIA. *An Ethnographic Account of Courtship, Marriage and Family Life among the Natives of the Trobriand Islands, British New Guinea.* 2 Vols.

By Bronislaw Malinowski.

Horace Liveright

\$10.00 for two volumes. New York

5 $\frac{1}{2}$ x 8 $\frac{1}{2}$; xxviii + 279 (Vol. I)

viii + 322 (Vol. II)

In these two beautifully printed and illustrated volumes Professor Malinowski has made a contribution to ethnography of the very first importance. Here one aspect or division of his studies on the Trobriand Island people is completely worked up, in full and satisfying monographic form. The plan and the scope of the treatment are indicated by the chapter heads: The relation between the sexes in tribal life; the status of woman in native society; prenuptial intercourse; the avenues to marriage; marriage; divorce and the dissolution of marriage by death; procreation and pregnancy in native belief and custom; pregnancy and childbirth; customary forms of license; love-making and the psychology of erotic life; the magic of love and beauty; erotic dreams and fantasies; morals and manners; a savage myth of incest.

The thing which perhaps is of greatest

general biological interest regarding the Trobriands is their ignorance of physiological paternity, a theme which Professor Malinowski has discussed in earlier works. Here he has developed it further with a wealth of detailed evidence. In doing this he uncovers a number of extremely puzzling observations regarding points in the physiology of human reproduction, the explanation of which is by no means clear.

Altogether the book is a notable one. We heartily agree with the statement made by Havelock Ellis in the preface:

These phenomena he views with a characteristically wide outlook; while not neglecting the precise technique of the erotic art among the Trobriand Islanders, he duly investigates their whole sexual life in its aesthetic, emotional, family, and social implications. Now that he has shown the way, other students doubtless will be inspired to follow. But in this field not all who are called are chosen. The special combination of needed qualifications can rarely be found, and meanwhile the opportunities are every year diminishing. It may safely be said that *The Sexual Life of Savages in North-western Melanesia* will become a classic of which the value must increase with the passage of time.



HAVELOCK ELLIS. *Philosopher of Love.* By Houston Peterson. Houghton Mifflin Co.
\$4.50 5 $\frac{1}{2}$ x 8 $\frac{1}{2}$; ix + 432 Boston

In *Havelock Ellis: A Bibliographical and Critical Survey* Isaac Goldberg gave us a pioneer study of one of the noblest and most significant figures of our age. In the present book Mr. Peterson, with the aid of unpublished documents and the co-operation of Ellis himself, paints a full-length portrait of his hero. We follow his development from the earnest boy, half comical, half pathetic, reared in the best traditions of English evangelicism, and aspiring to serve his God and his fellow men in the cure of souls, through the period of adolescent doubt in which he

sloughed off the orthodox beliefs of his boyhood, through his conversion, under the influence of James Hinton, to a vision of the universe as beauty, through his resolve to devote himself to making clear the problems of sex, a resolve followed *ohne Hast, ohne Rast* for more than thirty years through difficulties and obloquy which few men would have been willing to endure and bearing fruit in the classic series of *Studies in the Psychology of Sex*, and through his work as lay philosopher and interpreter of the art of life, to a ripe and serene old age. We do honor to Byrd and his fellow-explorers for facing hardships and perils in the quest of new geographical knowledge; it is meet and right that we should do greater honor to an explorer who has faced the suspicion of the compact majority and the persecution of narrow-minded officialdom in the quest of knowledge which would relieve some of the most poignant miseries from which mankind suffers.

Peterson makes it plain that Ellis was interested from the first in normal as well as abnormal sex psychology, and that it was largely owing to John Addington Symonds that the first volume of the *Studies* dealt with sexual inversion rather than with some other phase of the sex problem.



THE INTELLIGENT MAN'S GUIDE TO MARRIAGE AND CELIBACY.

By *Juanita Tanner*. *The Bobbs-Merrill Co.* \$3.50 6½ x 9½; xvii + 312. *Indianapolis*

The author of this book, writing under an assumed name, conceives herself to be the daughter of John Tanner, of *Man and Superman* fame, and grand-daughter of the author of that play. Her attempt, apparently, is to produce a counterpart to Shaw's guide for the intelligent woman in the field of socialism and capitalism. One

cannot but believe, however, that the really intelligent reader will lose patience before he has gone very far in these pages. To be sure, there is a certain amount of cleverness, but this soon wearies one. "Miss Tanner" has loosely thrown together a vast amount of material without making any clear cut development of the subject or any satisfactory presentation of facts. One reaches the conclusion that she probably favors "individual freedom" in the form either of a very loose family attachment or of celibacy since she says that

"All the things that are real fun, like travel and physical danger and rash utterances, demand a singleness of mind; they can not be complicated by any ordinary form of conjugality." "'For the wife and kiddies' a man will work fingers to the bone and brain to dullness; will swallow injuries and insult; will lie and steal and cheat his best friend and even commit murder; but he will not risk his life making great discoveries, or his neck breaking world's records, or his reputation stating unpopular truths."

Has she never heard of Palissy, the potter?



PHYSIOLOGIE GYNÉCOLOGIQUE ET MÉDECINE DES FEMMES.

By *H. Vignes*.

Masson et Cie

65 francs 6½ x 10; 565 (paper) *Paris*

This is a valuable addition to the literature of the physiology of reproduction. The material is arranged under eight general heads as follows: Primary sex characters; genital function before puberty; puberty and the realization of the sexual type; the adult woman; the menopause (spontaneous, surgical, radiation); statics of the female genital organs; influence of various hygienic and other environmental influences on the genital functions; the internal secretion of the ovary. The book is extensively documented, and well indexed.

BIOMETRY

STUDIES IN THE HISTORY OF STATISTICAL METHOD. *With Special Reference to Certain Educational Problems.*

By Helen M. Walker.

The Williams & Wilkins Co.

\$5.00 6 x 9; viii + 229 Baltimore

At this time, when the history of science is assuming more and more importance, Dr. Walker's book is especially welcome. That not all statisticians have an adequate knowledge of the history of their own *Fach* may be suspected from her note on recent discussions as to which of our contemporaries invented the "gross score" formula for the standard deviation, a formula first published by Encke in 1832. As its name implies, the book is not a general history of statistics, the development of official administrative statistics being merely sketched. Nor does it cover the development of all phases of statistical method. Nevertheless, we may be grateful to Dr. Walker for an excellent treatment of the history of some of the more important topics, especially the normal curve and correlation. Besides special bibliographies of memoirs on the probable errors of frequency constants, on measures of correlation other than the product-moment, and on the Theory of Two Factors, there is a bibliography of sources consulted in the preparation of the study and an index.



SCIENTIFIC METHOD. *Its Function in Research and in Education.*

By Truman Lee Kelley.

The Ohio State University Press

\$2.50 5 x 7½; 195 Columbus

The versatile and fecund Dr. Kelley publishes in this book a series of lectures originally delivered at Ohio State Uni-

versity, and dealing with scientific methodology, scientific ethics, the measurement of intelligence and achievement, curriculum construction, eugenics, and the mental traits of men of science. The last is an especially interesting application of the inductive method to the history of science.



HANDBUCH DER VERERBUNGSWISSENSCHAFT. *Lieferung 8. Band I. Variations-und Erblichkeitsstatistik.*

By Felix Bernstein *Gebrüder Borntraeger*

7.20 marks (Subscription) Berlin

14.40 marks (Single copies)

7 x 10½; iv + 96 (paper)

A brief exposition of probability and theory of statistics, followed by a more detailed development of the application of statistical methods to genetic problems. A valuable treatment of the subject, well worthy of the attention of geneticists.



PSYCHOLOGY AND BEHAVIOR

THE HISTORY OF PSYCHOLOGY.

By W. B. Pillsbury.

W. W. Norton and Co., Inc.

\$3.50 5½ x 8½; 326 New York

Dr. Pillsbury's history is a vivid reminder of how short a time it is since Psychology, under the alias of Mental Philosophy, was the boon companion of Moral Philosophy and other disreputable characters. There are those who suspect that in spite of its conversion and reformation it still retains a taste for doubtful company. Half of the book is devoted to the period before Fechner, a period in which psychology was for the most part subordinated to metaphysics and epistemology, and in which a rather crude in-

trospection was almost the only psychological method. The latter half of the book treats the seventy years since Fechner published his *Elemente der Psychophysik*, the first work to give psychology a definite experimental foundation, and several chapters are given to contemporary movements. To Pillsbury, as to W. H. R. Rivers, the phenomena of war shock are decisive against Freud's doctrine that the neuroses are always sexual in origin. His conclusion is that "psychoanalysis has had the effect of giving a more important place to the psychological attitude towards nervous diseases, and of emphasizing the fact that a patient's old conflicts and present emotional shocks are important factors in the development of neuroses. It stands as a strange episode in the history of psychology but one that has not been without many beneficial by-products."

Dr. Pillsbury is not a professional historian and cannot be fairly held to the standards of the historian. It is amusing, however, to read that Leibniz was "asked to report on the political events at the court of Frederick the Great." In 1716, when Leibniz died, the future Frederick the Great had attained the ripe age of four years. There were, therefore, probably not many political events at his court for Leibniz to report.



THE SOCIAL WORLD OF THE ANTS

Compared with That of Man. 2 Vols.

By *Auguste Forel*. Translated by C. K. Ogden.

Albert and Charles Boni

\$15.00 for two volumes. New York

5½ x 9; xlv + 551 (Vol. I)

xx + 445 (Vol. II)

These two large volumes represent practically seventy-five years of enthusiastic devotion to the study of this highly

organized group of insects. The author commenced his observations early in childhood. When he entered the university at Zurich he had already acquired a very wide knowledge of the behavior and habits of many forms of ants, and with his training as a physician, neurologist and psychologist, he was especially equipped to continue his studies, particularly in the field of sensory and instinctive behavior. There is much pleasure in store for the student and the amateur naturalist in these volumes. So much of the author's remarkable personality has crept into the writing of them that there is to be derived the kind of inspiration which rarely comes except through personal contact.

The work, in the main, is a collection of previously published material. It is divided into five parts, as follows:

- I. Genesis; Forms; Anatomy; Classification; Geography; Fossils.
- II. Feelings; Physiology; Ants and plants; Guests; Parasites; Nests.
- III. Apparatus; Foundation of colonies; Behaviour in the nests; Cattle; Gardens; Parasites.
- IV. Alliances and wars; Parabiosis; Lestobiosis; Slavery.
- V. Special customs; Epilogue.

Throughout the text there are numerous very excellent figures, and plates, both colored and black and white.



RÉVISION DE LA DOCTRINE DES LOCALISATIONS CÉRÉBRALES.

By *R. Brugia*.

Masson et Cie

24 francs

Paris

5¼ x 9¼; iii + 195 (paper)

Basing himself on the neurological experiments of Loeb and on the knowledge of cerebral trauma gained during the World War, Professor Brugia proposes to sub-

stitute for the doctrine of cerebral centers the segmentary or metameric theory of the nervous system, which holds that it

results from a colony of units (segments or metameres) in series; that each metamere is provided with a pair of nerves (neuromere), the one (ganglionic) a sensory nerve, leading from a cutaneous zone (dermatomere) or an organ of special sense, the other a motor nerve, ending in a muscular group (myomere); that there are *no centers*, every reaction being integrated by the whole of the segment, and being produced without the specific intervention of cellular elements; that co-ordination is based on the unitary and chain-like structure of the whole neuraxis, on the activity of the fibrils, perhaps uninterrupted and disposed in a closed network like that of the capillaries . . . ; that the cell bodies, not inherent but adherent, the fibrils passing through or around them, provide for generic functional activities, that is, contribute to the same conductivity which appertains to the fibers, and moreover serve *probably* . . . as accumulators and distributors of potential energy, and *undoubtedly* as means of nutrition, as is demonstrated by the degeneration of the axis-cylinder when the cells are separated or destroyed.

The book is well worthy of the attention of every neurologist. By the way, was it Augustine or Tertullian who wrote, "*Credo quia absurdum est*"?



THE PROJECTION OF THE ASTRAL BODY.

By Sylvan J. Muldoon and Hereward Carrington.

Rider and Co.

18 shillings net 5 $\frac{7}{8}$ x 9; 242 London

Mr. Muldoon, who has been a projector for twelve years, gives detailed directions in this book for projecting one's astral body. However, the reviewer regrets to report that in his own case following these directions has not yet produced results. There is an interesting passage on occult dietetics, quoted from an article by Prescott F. Hall in the *Journal of the American Society of Psychical Research*:

A vegetable diet tends to loosen the vibric matter of the astral body; and vegetables, fruits, and prunes

make the blood able to attract spiritual power. Carrots also are beneficial. Nuts, especially peanuts, are bad—especially near the time of sitting for development, as they tend to make one's atmosphere of one colour. Raw eggs are favourable. Liquids are favourable to development . . . Fasting often helps the liberation of the astral body.

Now we know why the inhabitants of boarding houses are so psychic. It is a result of their diet of prunes.



THE WAY WE THINK. *A Primer of Education and Psychotherapy by Reëducation.* By H. Travers Cole.

Occult Publishing Co.

\$2.00 (Regular Edition)

Chicago

\$3.00 (De Luxe Edition)

5 $\frac{1}{2}$ x 8 $\frac{1}{2}$; 171

A contribution to psychology from the realm of learning where osteopathy is medicine. It is taught that the rhythmic pulsation of the brain discovered by Vittoz is the physical sign of sufficiency of brain control. The rate is usually half the number of heart beats and twice the number of lung movements, and mounts to more rapid rhythms as thinking energizes the mechanisms of sensation, idea and act. By feeling in on the brain the unprejudiced physician can detect the irregular pulsation of the psychasthenic and has within his grasp the technique to effect prevention and cure.



SELECTIVE TRANSPORTATION BY CHIMPANZEES. *Comparative Psychology Monographs, Vol. 5, No. 4, Serial No. 26.* By Harold C. Bingham.

The Johns Hopkins Press

75 cents 6 $\frac{3}{4}$ x 10; 45 (paper) Baltimore

A report of a series of interesting tests on four chimpanzees who were put to work to solve the problem of moving food

from an inaccessible place within a wire cage to an opening where they could easily procure it. Food was suspended in the cage in such a way that it could be moved, by manipulation from the outside, to one of four openings near the base of the cage. Each animal was allowed ten minutes to find the solution. All failed the first time. Three succeeded in the second trial, while the fourth needed one more chance. A number of variations were later introduced to make the solution more complicated. The author believes that one of the most important contributions of these experiments is the "opportunity of seeing accidental, habitual and ideational behavior in immediate contrast." Space does not permit a detailed report of the results. The general conclusion which he reaches is that the behavior of the chimpanzees exhibits adaptive characteristics which are ideational.



THE PROCESS OF HUMAN BEHAVIOR.

By Mandel Sherman and Irene Case Sherman.
W. W. Norton and Co.

\$3.00 5½ x 8½; 227 New York

This book is the result of six years of study of the development of behavior in human infants. Direct observations were augmented by motion pictures. The book opens with two introductory chapters on the growth and significance of the nervous system. Then follows the discussion of the authors' investigations under the following headings: The first human responses; sensori-motor development; observation of the emotions; nature of the emotions; development of personality, and personality and social behavior. The authors present much interesting and original material. They have wisely excluded discussions of the various schools of psychology. The final paragraph in the

book briefly summarizes the conclusion which is reached by this study:

We have seen how adaptive behavior develops as a result of experience. Personality, then, which is made up of characteristic behavior, is especially fashioned by experience, for the process of human behavior is truly a developmental process of adaptation of the individual to his environment.



THE SCIENCE OF PSYCHOLOGY. *An Introductory Study.*

By Raymond H. Wheeler.

Thomas Y. Crowell Co.

\$3.75 5½ x 8½; xvii + 556 New York

An excellent general textbook of psychology. The chapter headings will indicate the plan of organization of the material. After an introductory chapter dealing with general definition, and a brief historical review, there follow chapters on: social behavior (two chapters); intelligent behavior (two chapters); emotive behavior (three chapters); learning behavior (three chapters); simple reaction, and observational behavior (two chapters); general summary. The point of view throughout is the organismal-conformationist. The book is well documented throughout, and carries detailed author and subject indices. It is a notable addition to the textbook literature of the subject.



DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

HANNO or *The Future of Exploration. Today and To-morrow Series.*

By J. Leslie Mitchell.

E. P. Dutton and Co.

\$1.00 4½ x 6; 94 New York

The second chapter of this book is a sane and interesting discussion of the

future of exploration in the Arctic and Antarctic, the Sahara, Arabia and other *terrae incognitae*. With Byrd's flight to the South Pole fresh in mind it is intriguing to come on Mr. Mitchell's conclusion that

for purposes of northern exploration the aeroplane has been much over-praised. It is no more an instrument of exploration than Herr Amundsen is an explorer. The trans-Arctic flights early in the present decade achieved nothing; they were mere exuberances of ignorance favoured by inexperience of climate. As a scouting and general survey instrument it has its uses under favourable conditions.

In the later chapters Mr. Mitchell's imagination, taking the bit in its teeth, reaches a goal much like one of the earlier novels of H. G. Wells. Not only will men penetrate the earth's crust to the subterranean seas and the great cavern which, he believes, occupies the interior; they will traverse the interplanetary spaces and explore the craters of the moon and the canals of Mars.



HERACLITUS or *The Future of Films. To-day and To-morrow Series.*

By Ernest Betts. E. P. Dutton and Co.
\$1.00 4½ x 6; 96 New York

This is not so much the author's projection of what the films are likely or inevitably to be as what he would like to see them be. It is an essay on the possibilities of the movies as a fine art as esoteric as that of Michelangelo. Mostly it is a plea for the free play of the creative spirit in the cinema as opposed to the present condition in which a hundred influences emanating from the box office dominate it. The author would simplify the movie theater itself and experiment with such things as the musical accompaniment and the introduction of sound. He envisages the movies of the future as pictorial poetry.

The book is done in a bouncing, entertaining style and contains one *mot* worth

quoting. Israel Zangwill is reported as saying that the whole movie is more important than the actress' part and the author adds, "*Sic transit Gloria Swanson.*"

[NOTE: Through the kindness of the well-known movie magnate, Mr. J. Pierpont Cohenheimer, the QUARTERLY REVIEW hopes to be able to offer a prize of \$100,000 (in Confederate money) for the best essay of not less than 5000 words stating *why* this was worth quoting.]



SCIENCE IN LITERATURE. *A Collection of Literary Scientific Essays.*

Edited by Frederick H. Law.

Harper and Bros.

\$1.20 5 x 7½; xvii + 364 New York

A collection of twenty literary, scientific essays to provide suitable material for College Entrance Requirements in English. A few of the titles, selected at random, are: Secret of the charm of flowers, by William Henry Hudson; Secrets of the ocean, by William Beebe; On a piece of chalk, by Thomas Henry Huxley; The discovery of radium, by Madame Marie Skłodowska Curie; The atomic theory, by Edward Neville da Costa Andrade; Electricity and civilization, by Charles Proteus Steinmetz; Pivotal figures of science, by Arthur Elmore Bostwick.



ATALANTA or *The Future of Sport. To-day and To-morrow Series.*

By G. S. Sandilands. E. P. Dutton and Co.
\$1.00 4½ x 6; 117 New York

To get a running start for the future of sport Mr. Sandilands devotes the greater part of his book—and to our notion the most interesting part—to the past and present of sport. We recommend to all lovers of the pugilistic art the account of the famous match between Tom Sayers and the Benicia Boy. There were giants in those days!

MRS. FISHER or *The Future of Humour.*
To-day and To-morrow Series.

By Robert Graves. E. P. Dutton and Co.
\$1.00 4½ x 6; 95 New York

If the humor of the future is as dull as
The Future of Humour God pity the people
of the future!



EDITORIAL NOTE

It has always been a deplorable fact
that American biologists have known

relatively little about the productive activities of their Russian colleagues. This is, of course, because of the language barrier. By the election to the Editorial Board of THE QUARTERLY REVIEW OF BIOLOGY of W. W. Alpatov, *Privatdocent* in the University of Moscow, and well known for his numerous publications in the fields of entomology, biometry and experimental zoology, it is hoped that the QUARTERLY REVIEW may contribute something towards a better interchange of knowledge between Russian and American biologists.



THE QUARTERLY REVIEW of BIOLOGY



EVOLUTION OF FACIAL MUSCULATURE AND CUTANEOUS FIELD OF TRIGEMINUS

PART I

By ERNST HUBER

Department of Anatomy, Johns Hopkins University

IN THE following chapters the author presents conclusions from detailed comparative anatomical, embryological and racial anatomical studies (1913-30) on the facialis musculature and on the cutaneous field of the *N. trigeminus*, correlated with data obtained from neuro-physiological investigations.

I. THE EVOLUTION OF THE FACIALIS MUSCULATURE FROM LOWER VERTEBRATES TO MAMMALS, WITH A DISTINCT GROUND PLAN IN THE MONOTREMES AND A COMMON GROUND PLAN FOR THE MARSUPIALS AND PLACENTALS

In order to present a comprehensive picture of the marvelous evolution of the facial musculature I shall briefly view conditions in a few selected types of the "ascending scale of Vertebrates," beginning with the Selachians, where the motor facialis field is represented by a comparatively insignificant muscle territory. While a series of scattered earlier publications by

Vetter, Tiesing, Stannius, Adams, Walter, Fischer, Ecker, Gaupp, Wiedersheim, Killian, Fürbringer and others referred to facial musculature of certain representatives of the lower Vertebrates, Ruge's classical monograph (1896) finally outlined the evolution of this muscle field in the main groups of the lower vertebrates up to the reptiles, with an attempt to link these with the monotreme mammals. This work of Ruge's afforded a solid basis for further elaboration of this fascinating chapter of comparative anatomy.

The writer has had opportunity to study representatives of the main groups of Vertebrates, including the fishes, amphibians, reptiles and birds of which only a few were examined, while concentrated efforts were directed towards a systematic investigation of the facial musculature in mammals.

Fishes: In the dogfish we find, connected with the branchial skeleton (fig. 1a) a number of serially arranged muscle sections forming the "constrictor musculature" of the gill arches (fig. 1b). This muscula-

ture is an intrinsic part of the respiratory apparatus. It effects the alternating constriction and distension of the branchial cavity, regulating at the same time the opening and closing of the spiraculum and the real gill clefts. The different segments of the "*M. constrictor superficialis*" are innervated through the 5th to the 10th cranial nerves. The second segment, the musculature of the 2nd branchial or hyoid arch, is situated between the spiraculum and the 1st real gill cleft. It is innervated by the N. VII. This small muscle territory represents the facialis musculature, which though already differentiated into several muscle portions, shows a most primitive arrangement.

With the understanding of this simple ground plan, we have the clue to the understanding of conditions found in the other groups of fishes, where further differentiations have taken place in connection with the transformations in the hyoid arch and the skull, and with the formation of a skeleton-supported operculum (fig. 1c) which covers the individual gill clefts (figs. 1a and b). Amongst the fishes, the bony fishes have reached the highest specialization (fig. 1c).

Amphibians: The perennibranchiate and derotremous amphibians show the most primitive conditions amongst this group. The superficial *M. constrictor arcuum viscerale* (fig. 2a) is here separated into different segments, corresponding to the various visceral (branchial) arches. The facial segment, originally a mere portion of the uniform "*M. constrictor superficialis*," has thus become independent, and moreover has reached a greater expansion cranialwards and caudalwards. It is divided into a superficial and a deep layer which, however, have retained their primitive connection dorsally. The deep layer (fig. 2b) is attached to the hyoid

bone, with another portion running to the mandible. The latter forms the functionally important *M. depressor mandibulae*.

Conditions found in the other groups of the amphibians can easily be understood from the ground plan already described. The anurous amphibians show great reduction of the superficial facialis musculature (compare figs. 2c and d), while the deep facialis musculature, especially the *M. depressor mandibulae*, is very well developed (fig. 2c).

Reptiles: From conditions typical of the primitive urodele amphibians, we can also understand the arrangement of facialis musculature in the reptiles. Here we find likewise a superficial and a deep layer which have kept their primitive connection dorsally. The deep layer (figs. 3b and d) shows an arrangement similar to that in the urodeles, but the superficial layer (figs. 3a and c) has gained a wider extension, in connection with the formation of a more definite neck region. Arising from the dorso-lateral fascia and extending, with or without interruption (fig. 3a contrasted with fig. 3c), ventrad to be inserted into the ventral median aponeurosis, it forms a well defined *M. sphincter colli*.

Birds: Having evolved from the reptile stem, this highly modified group shows conditions similar to those in the reptiles. There is likewise present a *sphincter colli*, which in long necked birds may show an enormous extension (fig. 4). In its course it covers the longitudinal trapezius muscle, to which it may be closely adherent.

Mammals: In the phylogeny of the Mammals fundamental changes have taken place, leading to a unique development of this muscle field.

In all mammals the superficial facialis musculature has given up its former connection with the deep facialis musculature, and the common innervation through

branches of the *N. facialis* remains the only indication that the two muscle groups belong together genetically.

The deep facialis musculature is in the Monotremes differentiated into the *M. stapedius* and *M. styloideus*, while the *M. detrahens mandibulae*, which occasionally has been included in this group, in reality belongs to the masticatory group (compare Huber, 1925, p. 6).

In the Marsupials and part of the Placentals the deep facialis musculature gave rise to the *M. stapedius* and to the posterior belly of the *M. biventer mandibulae* (fig. 6c), while in the rest of the placentals in addition to these muscles, a *M. stylo-hyoideus* has shed off from the deep facialis muscle mass, and furthermore in some forms a *M. jugulo-hyoideus* (fig. 6f). The morphology of the latter is not yet clear (Huber, 1924-25, p. 369, footnote). The *M. biventer mandibulae*, on the other hand, shows manifold modifications and adaptations, which have been dealt with in a large series of publications by various authors (see Huber, 1924, p. 190, ff.).

After having completely become separated off from the deep facialis musculature, the "primitive *Sphincter colli*" of the promammalian ancestors, gave rise to the superficial facialis musculature of the mammals. The monotremes (fig. 5) developed along their own line, on a ground plan which is distinctly different from the common marsupio-placentalian ground plan (fig. 6). The superficial facialis musculature gradually expanded over the whole head and gained extensive connections with the freely movable skin. The formerly rigid mask thus became mobile. Certain muscle portions became connected with the newly formed (in the marsupials and placentals movable) outer ear; others grouped around the eyes, and still others attached themselves to the snout.

The striking difference in the snout mus-

culature of the monotreme and marsupio-placentalian plan is in close relation with fundamental differences in the construction of the snout. In *Echidna*, which in this respect shows the more primitive conditions of the two monotremes, the intermaxillary bones are not only intercalated between the maxillary bones but they surround with their prenasal processes a large part of the cartilaginous skeleton of the nose. Posteriorly these processes join with the nasal bones, with which they form the bony roof of the nose (compare fig. 22c). The cartilaginous skeleton of the nose in *Echidna* is thus largely enclosed in a bony framework built up by the maxillary, intermaxillary and nasal bones, and the tip of the snout is rigid as in the reptiles. In *Ornithorhynchus*, modifications of the monotreme plan have taken place in connection with the formation of the bill (see chapter V and figs. 22a-d), which is likewise a rigid structure. In the marsupials and placentals on the other hand through reduction of the bony framework (i.e., through the loss of the prenasal process of the intermaxillary bone), the cartilaginous skeleton of the nose became to a large extent free, and the tip of the nose became movable through facial muscles which insert there.

Other muscle portions then muscularized the newly formed *vestibulum oris* with the bordering lips. Thus a large number of more or less distinct superficial facialis muscles were formed.

It is to be expected that all these individual muscles are innervated by branches of the *N. facialis*, the nerve of the "primitive *Sphincter colli*," which muscle, contrary to the views of Boas and Paulli (see Huber, 1922-23, p. 92-93), is the matrix of the entire superficial facialis musculature. Such an innervation of the superficial facialis musculature exclusively through the *N. facialis* has been doubted by

a series of authors who claimed an additional nerve supply to some of the superficial facialis muscles, by branches from the cervical plexus and *N. trigeminus*. But these doubts were eventually disproven on an experimental basis (Michelson, 1922; Huber, 1924; Huber and Hughson, 1926).

Embryological development gives further evidence that the superficial facialis musculature is the genetically uniform field of the *N. facialis*. Though our knowledge of the embryology of the field is still very incomplete, a valuable start has been made through the investigations of K. Rabl (1887), G. Killian ('90), J. Popowsky ('95), H. Baum and R. Dobers (1905), H. Rouvière ('06), R. Futamura ('06, '07), W. H. Lewis ('10), F. H. Edgeworth ('14, '23), M. Zuckermann-Zicha ('25), Huber (chapter 7), and others. Through these contributions we learn that in mammals the facialis muscle field starts its development from a small muscle anlage, connected with the hyoid arch. From this primitive anlage split off the deep and the superficial facialis musculature. The latter then leaves its originally restricted territory in the neck region and invades the face, where it differentiates into the many more or less distinct individual muscles. Following this differentiation in the muscle field, the *N. facialis* ramifies, and gradually forms the complicated facial plexus. The embryological development of the facialis musculature of the mammals, including man, thus recapitulates important stages of the phylogenetic development.

The *comparative anatomy and phylogeny* of the mammalian superficial facialis musculature is far better known than its embryology. Initiated through the monumental pioneer work of G. Ruge (1885, '87) a large series of publications on this subject have appeared by Tataroff (1887),

Süssmayr ('88), Popoff ('90), Schulmann ('90/91, '05), Ruge ('95, '11), Popowsky ('88, '93, '97), Bovero (1903), Baum and Kirsten ('04), Boas and Paulli ('08), Virchow ('08, '15, '23, '24, '27), Bluntschli ('09), Eisler ('12), Ückermann ('12), Huber ('18-30), Michelsson ('21), Paugger ('23), Sullivan and Osgood ('21), Lightoller ('25, '28), Schreiber ('28, '29), and many others. Moreover, much detailed knowledge on the human mimetic musculature with its innumerable individual variations (see Testut, 1884; Le Double, '97; Vilhena, 1911; Eisler, '12; *et alii*) has gradually been accumulated in continuation with the studies of the pioneers among the anatomists dating from the Renaissance (Vesalius, Eustachius, Albinus, Santorini, Sömmering, Cruveilhier, Henle, Gegenbaur). But even with this large amount of literature the field is merely outlined.

Through the investigations of Ruge (1895), Schulmann ('05), Boas and Paulli ('08), Huber ('30), and others, it became known that already in the *Monotremes*, in these most archaic, strangely specialized mammals, the superficial facialis musculature is well developed and specialized (compare figs. 5, 13c and d). The monotremes, as already indicated, show features of their own. It is indeed impossible to homologize strictly the various groups of their facial muscles with those of the marsupials and placentals.

While the phylogeny of the superficial facialis musculature of the monotremes is still imperfectly understood we have now, owing to detailed, painstaking studies of various investigators, a fair knowledge of the evolution of this muscle field in the *Marsupials and Placentals*. In several previous publications (Huber, 1918, '22/23, '24; Huber and Hughson, '26) the author has given data upon which his conception of the derivation of the superficial facialis musculature was based.

The author's concept differs in fundamental points from the concept of Ruge (1885, '87), which was until most recent times almost generally accepted. The new concept may here briefly be summed up: From the "primitive *Sphincter colli*" restricted to the neck region as it still is in the modern reptiles and presumably was in the reptilian ancestors of the marsupials and placentals, there have shed off the undifferentiated platysma and *sphincter colli profundus*. These two primary muscle layers invaded the face, where they subsequently differentiated into the more or less distinct facial muscles. The platysma evidently gave rise to the *M. platysma colli et faciei*, and to the postauriculo-occipital muscle group, which includes part of the extrinsic and intrinsic ear muscles (figs. 6a and b). The rest of the superficial facialis musculature was derived from the *sphincter colli profundus* (figs. 6c and d).

According to Ruge's concept, based on his fundamental investigations on primates, the musculature of the cheek walls and lips alone was considered to be derived from the *sphincter colli profundus*, while the rest of the superficial facialis musculature was believed to have arisen from the platysma.

However, through more recent, largely unpublished investigations on representatives of marsupials and a large series of placentals, the author has obtained ample

evidence that the *sphincter colli profundus* must have played a far greater rôle as the matrix for the superficial facialis musculature than Ruge had assumed (compare figs. 7—11). This has most recently been demonstrated beyond doubt to conform with conditions found in the primates (Schreiber, 1928; Huber: figures of chapter 7).

The general plan of the superficial facialis musculature in the Marsupials (Boas and Paulli, 1908; Huber, '25, '30, and others) and primitive Placentals is strikingly similar (Huber), no doubt because the marsupials and placentals are closely related groups.

A thorough understanding of the morphology of the superficial facialis musculature of the more primitive placentals enables us to understand conditions found in the higher Placentals (compare chapter 7 on primates). In the various orders of the placentals the superficial facialis musculature has become specialized to different degrees and along many and very different lines. Even when secondarily reduced or in a vestigial stage, it affords material for far reaching evolutionary conclusions. The superficial facial musculature of mammals is also of high systematic value. Although not yet recognized, it has an importance similar to that of the skull, the teeth and the extremities.

FIG. 1. REPRESENTATIVES OF THE FISHES SHOWING THE INSIGNIFICANT MOTOR FIELD OF THE N. FACIALIS AS PART OF THE BRANCHIAL SKELETON MUSCULATURE

a. Embryo dogfish (modified after Braus). The branchial skeleton is exposed with the serially arranged anlagen of the constrictor musculature of the branchial arches. The section situated between the mandibular and the hyoid arches represents the muscle territory of the *N. facialis*. Note the relation of this muscle segment to the spiraculum in front and to the first real gill cleft behind. The subsequent muscle segments show a similar arrangement.

b. The branchial skeleton musculature of an adult dogfish (after Ruge). C₁, connected with the mandibular arch, is the muscle territory of the *N. trigeminus*; C₂, the musculature of the hyoid arch (*facialis* musculature) is bounded in front by the spiraculum, behind by the first real gill cleft; C₃ is the muscle field of the *N. IX*; while C₄-7 are under the domain of the *N. X*.

c. *Esox lucius*, a representative of the bony fishes (after Vetter), showing the complexity which has developed in the branchial skeleton musculature in connection with the formation of a skeleton supported operculum, which covers the gill clefts. Portions of the *facialis* musculature are adapted to the opercular skeleton.

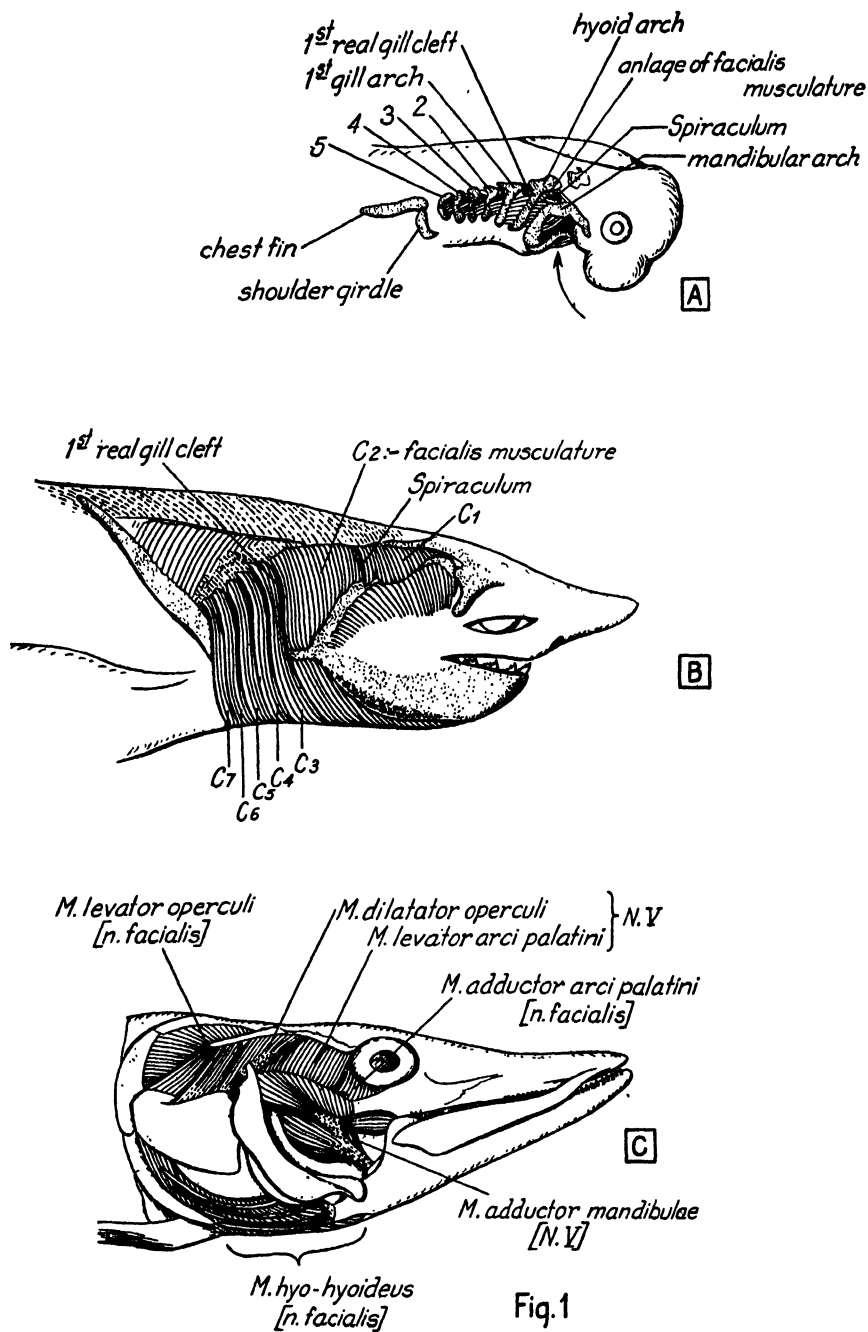


Fig.1

FIG. 2. FACIALIS MUSCULATURE IN AMPHIBIANS

a & *b*. *Menopoma*, a primitive representative of the urodele amphibians (modified after Ruge). The various sections of the *constrictor arcuum visceralium* have become independent and are further elaborated. Cz., the muscle territory of the N. *facialis*, has with its superficial layer expanded cranialwards and caudalwards. It partly covers the muscle territory of the N. V in front and that of the N. IX behind (fig. 2a). The deep facialis musculature (fig. 2b) has remained in connection with the hyoid arch, and by a portion is attached to the mandible (*M. depressor mandibulae*).

c & *d*. *Rana* as representative of the anurous amphibians (after Gaupp). The superficial facialis musculature has deteriorated, while the deep facialis musculature is represented by a well developed *M. depressor mandibulae* (fig. 2c) and by an intermandibular muscle portion (fig. 2d).

FIG. 3. FACIALIS MUSCULATURE IN REPTILES

The figures show the remarkable expansion of the superficial facialis musculature over a large area of the neck. It forms a characteristic "*Sphincter colli*." In *Varanus* (fig. 3a, after Ruge) this muscle layer is separated into a dorsal and a ventral part by a horizontal tendinous intersection. In *Lacerta* (fig. 3c, after Huber), however, the *sphincter colli* remains a uniform muscle layer.

b & *d* show the deep facialis musculature of *Varanus* and *Lacerta* with a well developed *M. depressor mandibulae*. Notice that superficial and deep facialis musculature has retained the primitive connection dorsally just as in the urodele amphibians. This primitive connection together with the characteristic innervation through branches of the N. *facialis* clearly indicate that both the superficial and deep facialis musculature belong to a phylogenetically uniform muscle field.

FIG. 4. FACIALIS MUSCULATURE IN BIRDS (AFTER FÜRBRINGER)

The birds having evolved from the reptile stock show an arrangement of the facialis musculature similar to that of reptiles. The superficial facialis musculature is likewise represented by a *sphincter colli*, which in long necked birds, such as the goose (see figure), shows an enormous extension. It may secondarily fuse with the subjacent *M. trapezius*, which has occasionally been mistaken for the homologue of the platysma of mammals. Noteworthy is the fact that in the birds, as in the reptiles and amphibians, the superficial facialis musculature has not expanded forward beyond the ear-drum. The face is bare of voluntary musculature, and thus remains a rigid mask, this in striking contrast to the mammals (compare following figures).

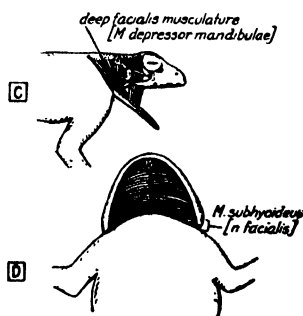
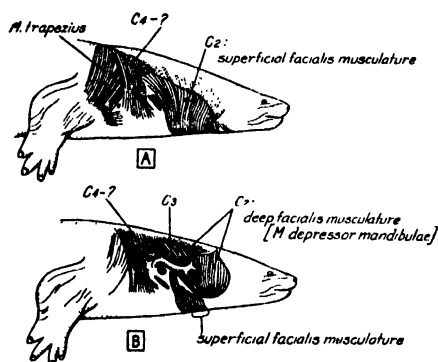


Fig. 2

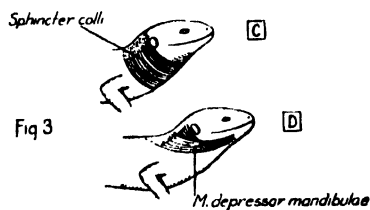
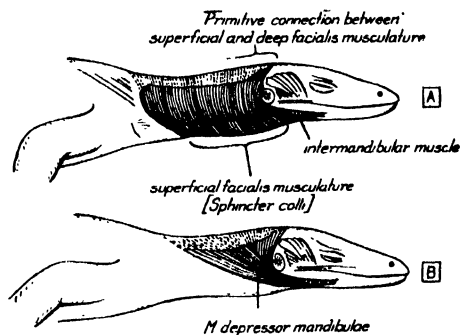


Fig. 3

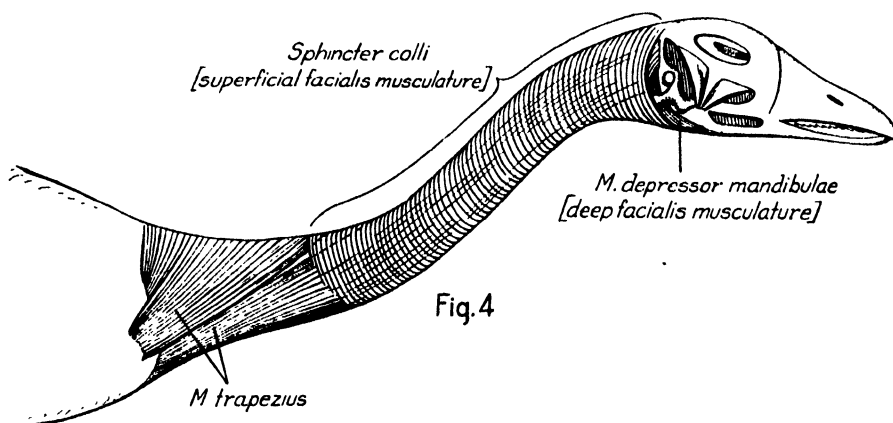


Fig. 4

FIG. 5. FACIALIS MUSCULATURE IN MONOTREME MAMMALS (ECHIDNA AND ORNITHORHYNCHUS SIVE PLATYPUS)

The superficial facialis musculature is no longer restricted to the neck region, but has expanded into the face, where it has become differentiated into muscle groups connected with the ear, eye and snout. Although there are notable differences in *Echidna* and *Ornithorhynchus*, the arrangement of their facial muscles can be derived from a common ground plan, which is peculiar to the monotremes and fundamentally different from the marsupio-placentalian ground plan of fig. 6. Characteristic for both *Ornithorhynchus* (fig. 5a) and *Echidna* (fig. 5d) is a powerful longitudinal layer ("platysma") which has expanded from the nuchal region caudalwards over the anterior part of the back, while oralwards it continues towards the ear and below this into the face, as far as the base of the greatly modified, rigid snout. Here it is firmly attached (*Ornithorhynchus*, figs. 5b & c; *Echidna*, fig. 5e). A very powerful portion deviating from the most caudal section of the longitudinal layer has become inserted into the fore limb (a and d). In *Echidna* (d) this limb portion is reinforced by additional powerful muscle portions, which have shed off from a deep stratum of the common longitudinal muscle mass in the nuchal region (see further fig. 13c). The bulk of this extremity musculature of the facialis field is very considerable, especially in *Echidna*. Characteristic of both monotremes, *Ornithorhynchus* (fig. 5a) and *Echidna* (figs. 5d, 13c and d), are the expansion of the facialis musculature caudalward into the domain of the *panniculus carnosus*, and the interlacing and partial fusion of these two genetically distinct muscle territories. This intimate relationship has led to the erroneous concept that the superficial facialis musculature is merely the forward extension of the *panniculus carnosus*.

In both monotremes the powerful *sphincter colli* is a striking feature. In *Ornithorhynchus* (a) this layer is in its entire expansion situated externally to the "platysma." It extends as a continuous layer from the shoulder region forward close to the base of the snout. In *Echidna* the *sphincter colli* (fig. 5d, more fully shown in figs. 13c and d) covers with a ventral portion (fig. 13d) a considerable part of the fore limb, into which it inserts with its most caudal bundles. The cranial continuation of the *sphincter colli* (fig. 5d, 13c and d) overlaps with some bundles the "platysma" dorsally, while other bundles dip under it. These deep bundles of the *sphincter colli* ascend to the posterior margin of the ear cartilage, where they insert. The rest of the *sphincter colli* from the ear on forward is situated externally to the "platysma" layer (figs. 5d and e, and 13c). It extends as far as the base of the snout, thus showing an extension similar to that in *Ornithorhynchus*.

It is noteworthy that both monotremes lack a continuous *sphincter colli profundus*, which is so characteristic of the marsupio-placentalian ground plan. It is not at all certain whether the *M. sphincter bursae buccalis* of *Ornithorhynchus* (fig. 5c) and the *M. "buccinator"* of *Echidna* (fig. 5e) really represent differentiations of a *pars oris sph. colli profundus*, as has been assumed by former authors. It is more probable that these muscles have arisen from the longitudinal layer at the base of the snout, where this layer inserts into the maxilla with a heavy, coarse bundle mass. Fig. 5b shows in *Ornithorhynchus* the inserting portion of the "platysma" after partial removal of the external *sphincter colli*. It may be seen that the "platysma" forms a large part of the musculature of the buccal pouch. Posteriorly bundles have settled down on the lateral wall of the pouch, while the middle portion of the "platysma" evidently through the herniation of the pouch has thinned out and has in part become subsequently deteriorated. This leaves the most oral section of the middle portion of the "platysma" as a feeble bundle layer, which inserts into the angle of the mouth. A stronger portion of the "platysma" is applied to the wall of the buccal pouch below. It inserts anteriorly with little tendons into the shield-like flap of the lower jaw. The main mass of the "platysma" strengthens the buccal pouch above, and inserts with a mass of heavy coarse bundles into the maxilla. Deeper bundles of this inserting portion of the "platysma" (fig. 5c) deviate to form the *M. sphincter bursae buccalis*, which continues anteriorly into the *M. plicae anguli oris*, the sphincter muscle of the shield-like flaps of the bill. In *Echidna* (fig. 5e) the longitudinal layer inserts with heavy, coarse bundle masses all along the zygomatic arch and to the maxilla at the base of the snout. Deeper bundles of this inserting portion of the "platysma" deviate ventralward, forming a weak, vestigial layer. Splitting off from this layer there is a continuous muscle layer ("*M. buccinator*") spread out between the upper and the lower jaw. This "*M. buccinator*" extends forward as far as the tip of the slender snout, where it encircles the small oral slit.

The difference in the formation of the snout musculature in the two monotremes is obviously the result of divergent specialization, i.e., the great elongation of the snout in the ant-eating *Echidna*, and the formation of a bill and acquisition of a buccal pouch for storing grinding material (grit) in the aquatic, bottom feeding *Ornithorhynchus*.

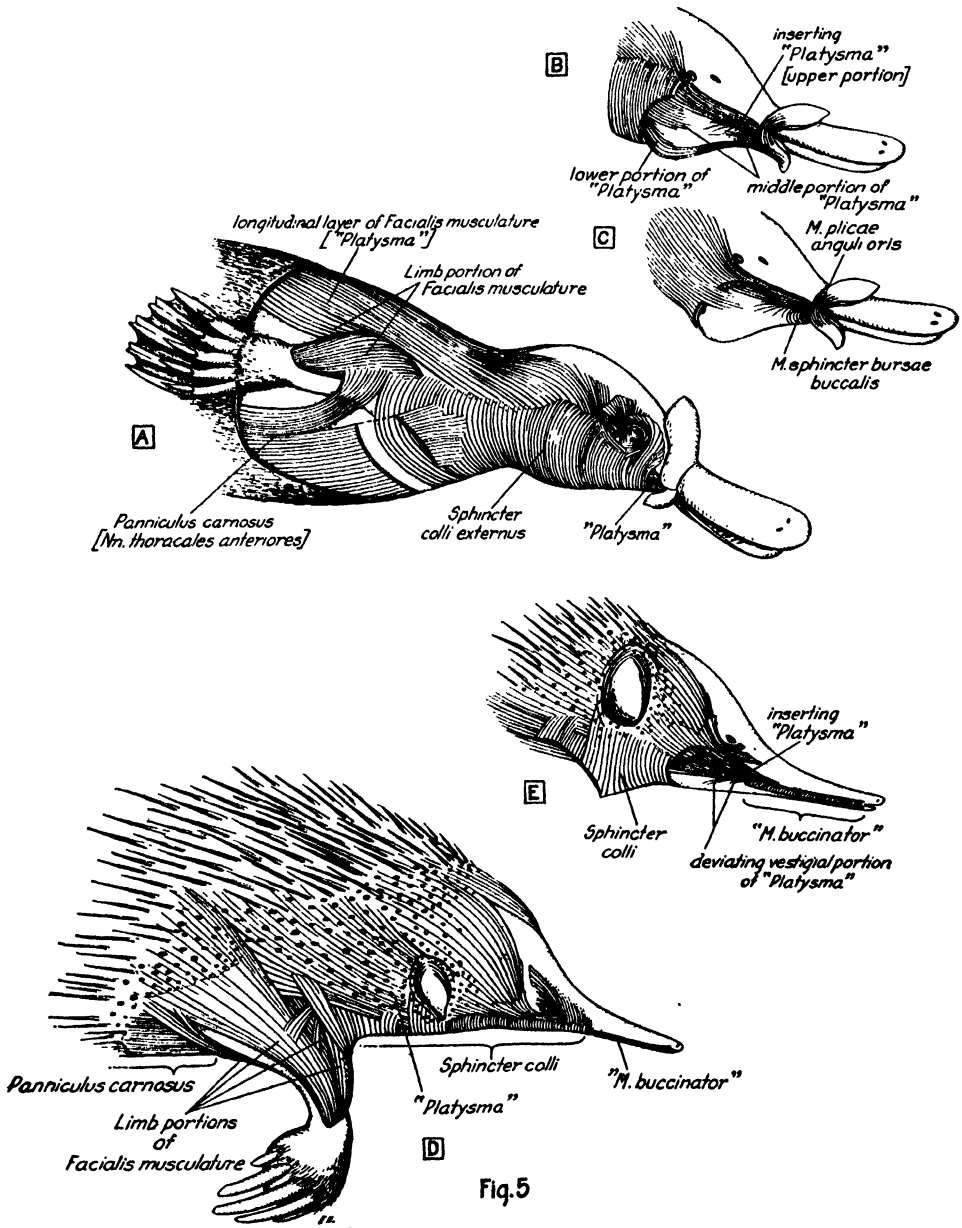


FIG. 6. SCHEME OF THE GROUND PLAN OF FACIALIS MUSCULATURE COMMON TO MARSUPIALS AND PLACENTALS

a-d. Superficial facialis musculature. From the "primitive *Sphincter colli*," the homologue of the *sphincter colli* of the reptilian plan, the platysma and the *sphincter colli profundus* have shed off. These two primitive muscle layers invaded the face, where they subsequently gave rise to the many, more or less distinct individual facial muscles. The platysma (fig. 6a), arising from the primitive *sphincter colli* in the nuchal region, gives origin to the *M. platysma colli et faciei* and the postauriculo-occipital musculature, which includes extrinsic and intrinsic ear muscles; some of these muscles (fig. 6b) have intruded into the preauricular territory. The *sphincter colli profundus* (figs. 6c and d), directly continuous with the "primitive *sphincter colli*," gave rise to the rest of the superficial facialis musculature, i.e., the preauriculo-temporo-frontal muscle complex, the musculature around the eye, and the muscles connected with the nose, lips and cheek wall. In some representatives of the placentals ventral bundles of the "primitive *sphincter colli*" overlap the platysma, thus forming a *sphincter colli superficialis* (fig. 6a). This layer has not given rise to individual facial muscles.

e & f. Deep facialis musculature, having completely separated from the superficial. Fig. 6e shows conditions found in the marsupials and in some primitive placentals, while in the other placentals (fig. 6f), a *M. stylo-hyoideus* has been formed in addition to the *M. biventer posterior*, and there is often a *M. jugulo-hyoideus* present. The tiny *M. stapedium* enclosed in the middle ear, is to be included in the deep facialis musculature.

g & h. *N. facialis*. The entire muscle field illustrated in figs. 6a-f is exclusively innervated by branches of the *N. facialis*, as demonstrated through morphological and experimental investigations. The ramification of the facial nerve follows the phylogenetic differentiation of the muscle field. We thus find that separate facial branches supply the various pre- and postauricular complexes of the superficial facialis musculature, and others the deep facialis musculature. Anastomoses between individual branches of the facial nerves form the plexus *facialis*.

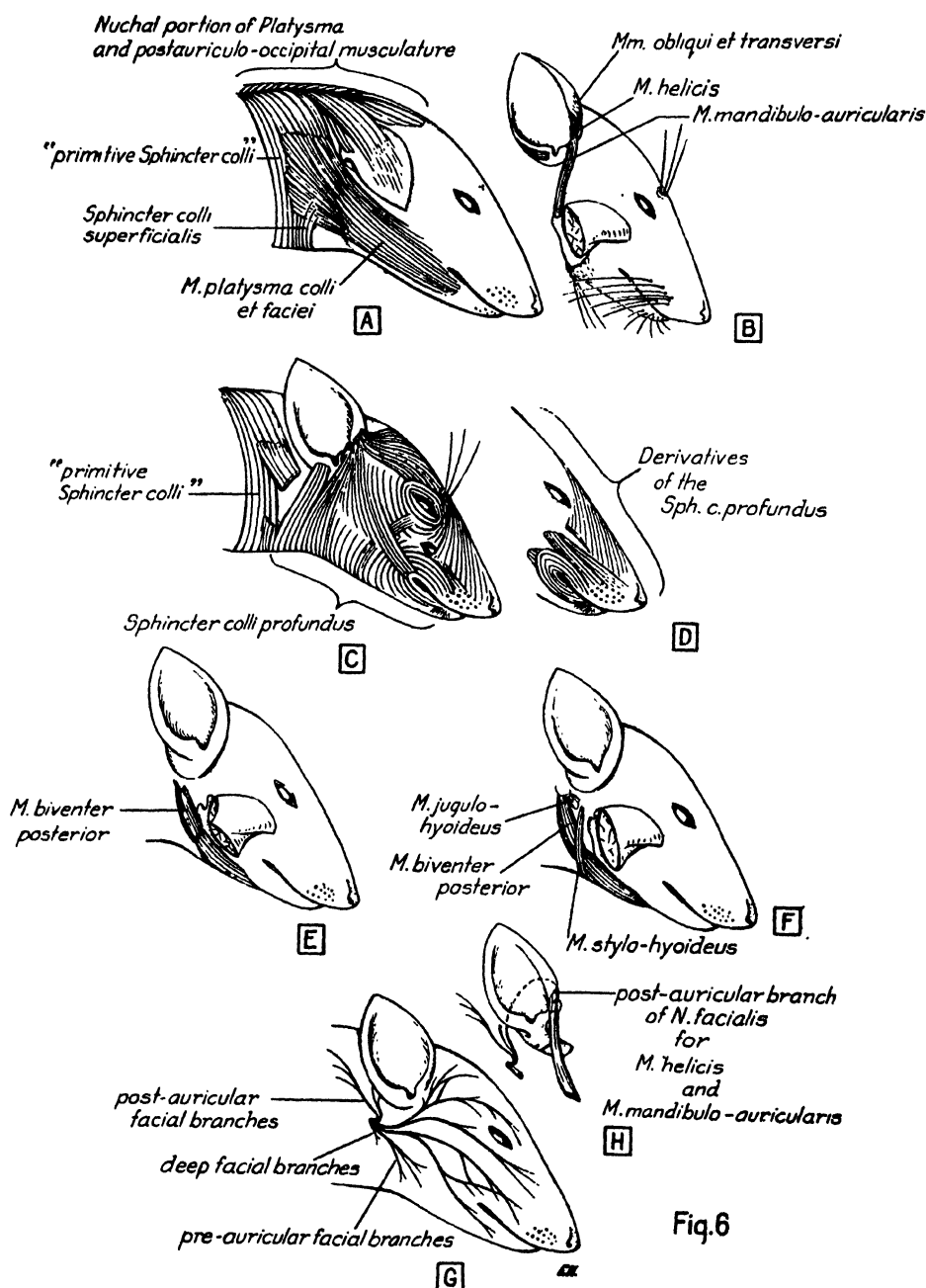


Fig.6

FIG. 7. *DIDELPHYS MARSUPIALIS* (OPOSSUM) REPRESENTING THE POLYPROTODONT MARSUPIALS (JOHNS HOPKINS COLLECTION)

a. Platysma and postauriculo-occipital musculature. Although the "primitive *sphincter colli*," the primary source of the entire superficial facialis musculature (compare fig. 6), has in the opossum been dropped from the plan of the superficial facialis musculature, the platysma still arises in the primitive way by a deep bundle layer from the nuchal region. The superficial bundle layer, on the other hand, has secondarily expanded caudalward into the shoulder region. Superficial and deep layers unite to form the well developed plate of the *M. platysma colli et faciei*. In the figure, the ear is shown pulled forward, to demonstrate the postauriculo-occipital muscle group which has retained the primitive connection with its matrix, the nuchal portion of the platysma. The additional small figure (*b*) shows the ear turned back to illustrate the *M. helicis* and *M. mandibulo-auricularis* of the post-auricular group, which have secondarily intruded into the pre-auricular territory (see the topographic relation of these two little muscles to the muscles of the pre-auricular group in fig. 7c).

c-s. The *sphincter colli profundus* and its derivatives. The *sph. colli profundus* forms a continuous transverse muscle layer (fig. 7c). In front of the ear the preauricular muscles have remained in broad primitive connection with their matrix, the *pars pre-auricularis sph. colli profundus*. The musculature of the face proper is yet little differentiated. The musculature of the snout, derivatives of the *pars oris sph. colli profundus* (fig. 7d & e), on the other hand, is differentiated and specialized. Note the muscle portions which are attached to the follicles of the supraciliary and cheek vibrissae (figs. 7a & c), to the mystacial vibrissae and to the vibrissae of the chin (figs. 7a, c & d). In contrast to the monotremes, the marsupials like the placentals possess a large spoon-shaped outer ear, with a well differentiated muscle apparatus composed of derivatives of both the post- and pre-auricular muscle groups (figs. 7a, b, c). A little shield (*scutulum*) of dense connective tissue has formed within the pre-auricular musculature, which allows these muscles to glide over the subjacent deep temporal fascia (figs. 7b & c). The scutulum of the opossum is, however, not as definite a structure as the similarly placed cartilaginous scutulum of representatives of certain orders of the placentals, such as the bats, lagomorph rodents (Leporidae and Ochotonidae), ungulates and carnivores (compare cat, fig. 11b; see further Huber, 1924/25, p. 370).

EVOLUTION OF FACIAL MUSCULATURE

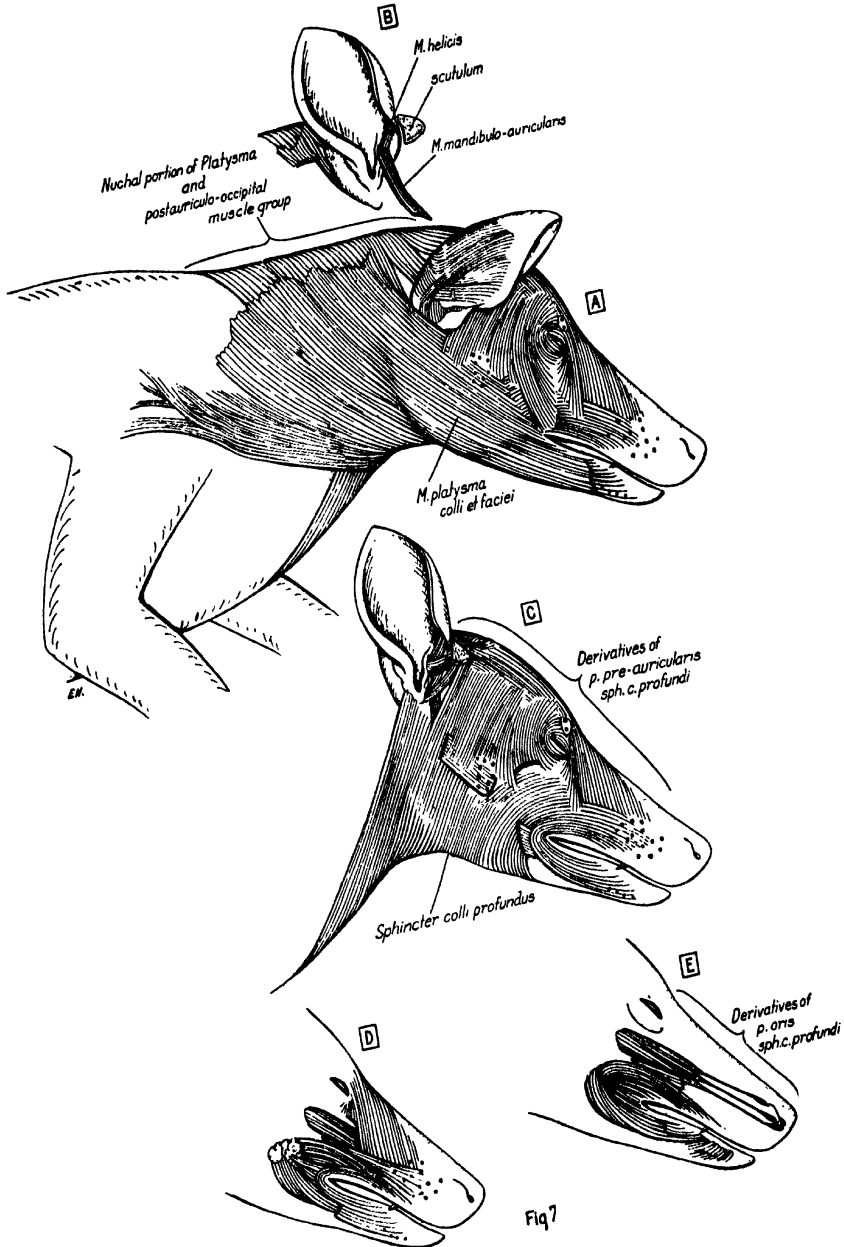


FIG. 8. *MACROPUS RUFUS* (KANGAROO) REPRESENTING THE DIPROTODONT MARSUPIALS (JOHNS HOPKINS COLLECTION)

Individual variations on the right and left side illustrating a first step of emancipation of the pre-auricular musculature from its matrix, the *pars pre-auricularis* of the *sphincter colli profundus*.

a. The platysma with primitive origin from the nuchal region is cut away in order to show the *sphincter colli profundus*. This forms a uniform transverse muscle layer with its most anterior portion (the *pars oris*) encircling the mouth cleft. The dorsal section of the *pars pre-auricularis sph. colli profundus* has become separated from the *sphincter colli profundus* layer; and subsequently some of its caudally deviating bundles came to overlap adjacent muscle portions,—in this case the *pars auris sph. colli profundus*. The same evolutionary trend is noticed in many placentals which still possess a *sphincter colli profundus* (compare e.g., lemur, chapter 7). This first step of involution of the *sphincter colli profundus* layer may be followed by complete deterioration of this layer, as seen in the higher platyrrhine monkeys and in all catarrhines (compare figures of chapter 7).

b shows the original condition: the dorsal section of the *pars pre-auricularis sph. colli profundus* remained part of the continuous transverse muscle layer of the *sphincter colli profundus* just as in the opossum (fig. 7c), and in other primitive marsupials examined by the author.

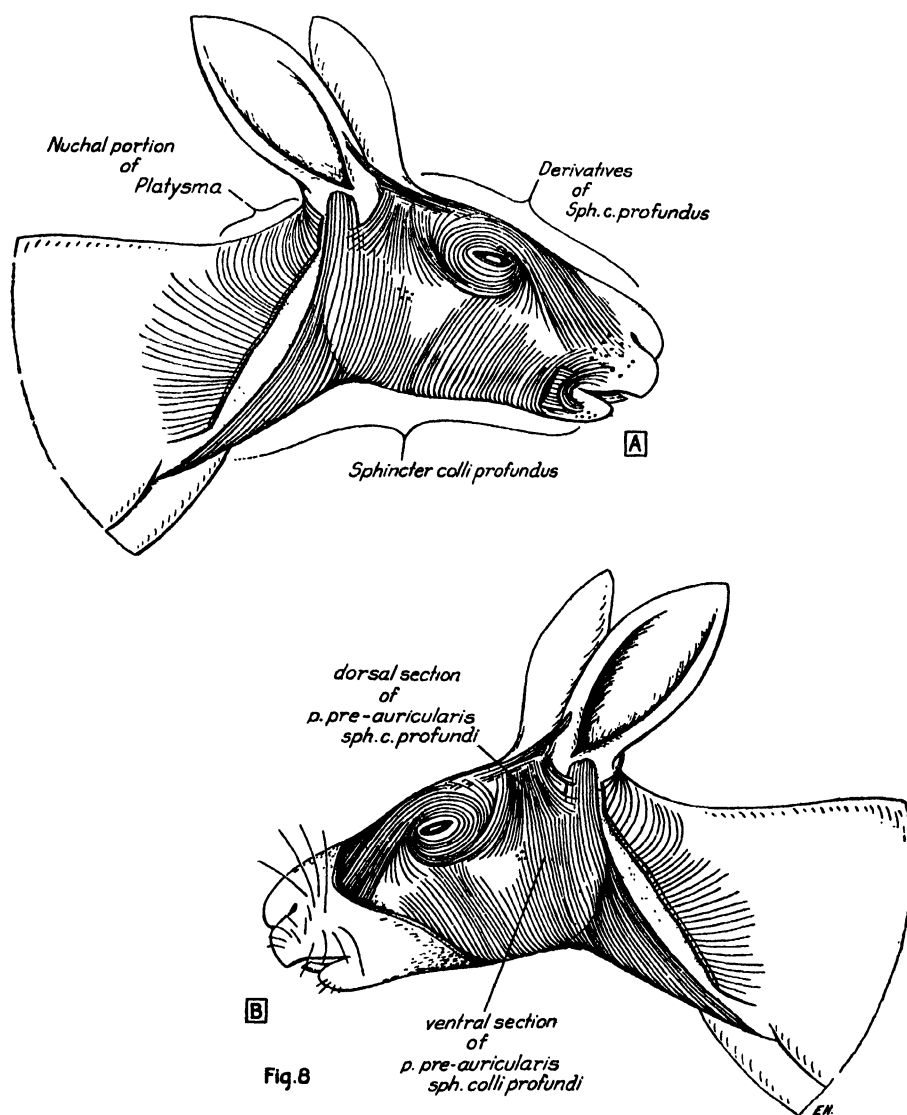


FIG. 9. THE GROUND PLAN OF THE SUPERFICIAL FACIALIS MUSCULATURE IN THE CAT AS A REPRESENTATIVE OF THE PLACENTALS (A AND B FROM THE SAME SPECIMEN; C FROM ANOTHER)

a. Restricted to the neck region is shown the "primitive *sphincter colli*," which is the primary source of the entire superficial facialis musculature. From the "primitive *sphincter colli*" arises in the nuchal region the platysma, from which the postauriculo-occipital muscle group has evolved. The latter has remained in primitive connection with its matrix. (Further details of the post-auriculo-occipital group are given in Fig. 10.) Ventrally on the neck a few muscle bundles cranial to the "primitive *sphincter colli*" overlap the platysma, thus forming a *sphincter colli superficialis*. This muscle layer is much better developed in the dog, which shows a ground plan similar to that of the cat (compare Huber, 1922/23). Just beneath the platysma is the *sphincter colli profundus*, which extends as a deep, transverse muscle layer as far as the mouth cleft. (It is shown in full extension in Fig. 9c.)

b. The superficial layer of the nuchal portion of the platysma is here cut off in order to show the deep layer in primitive connection with its matrix the "primitive *sphincter colli*." Superficial and deep layers of the platysma fuse to form the uniform *M. platysma colli et faciei*, which passes as a horizontal layer below the ear into the face and forward as far as the mouth cleft and for a short distance into the lower lip.

c. The platysma, except its nuchal portion, has been removed in order to expose the *sphincter colli profundus*, which has given rise to the superficial muscles of the face proper (compare further fig. 11).

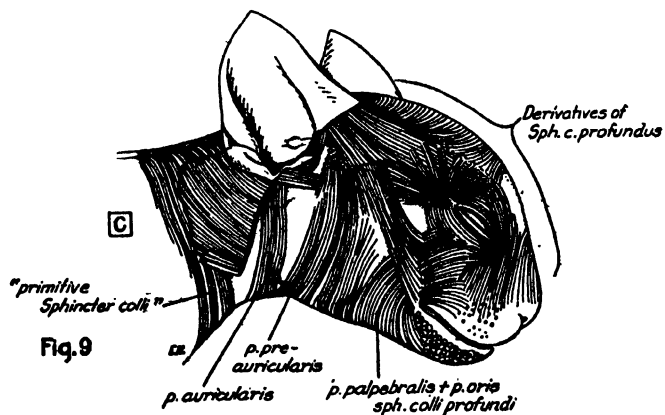
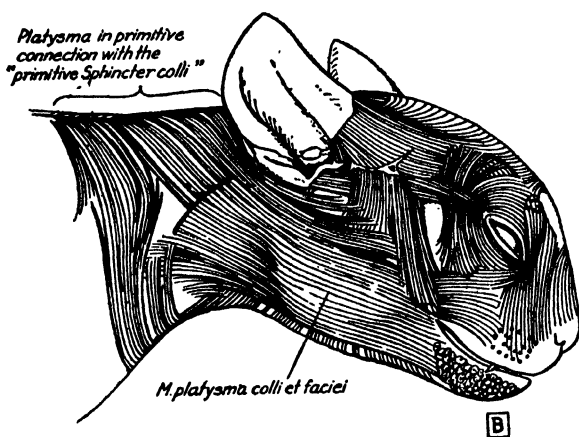
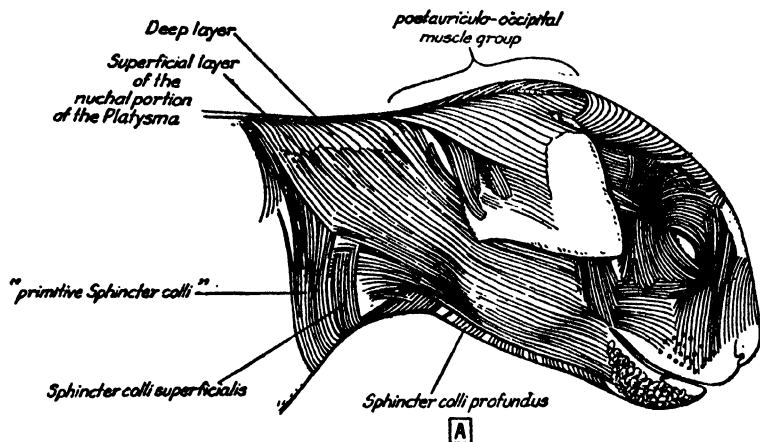
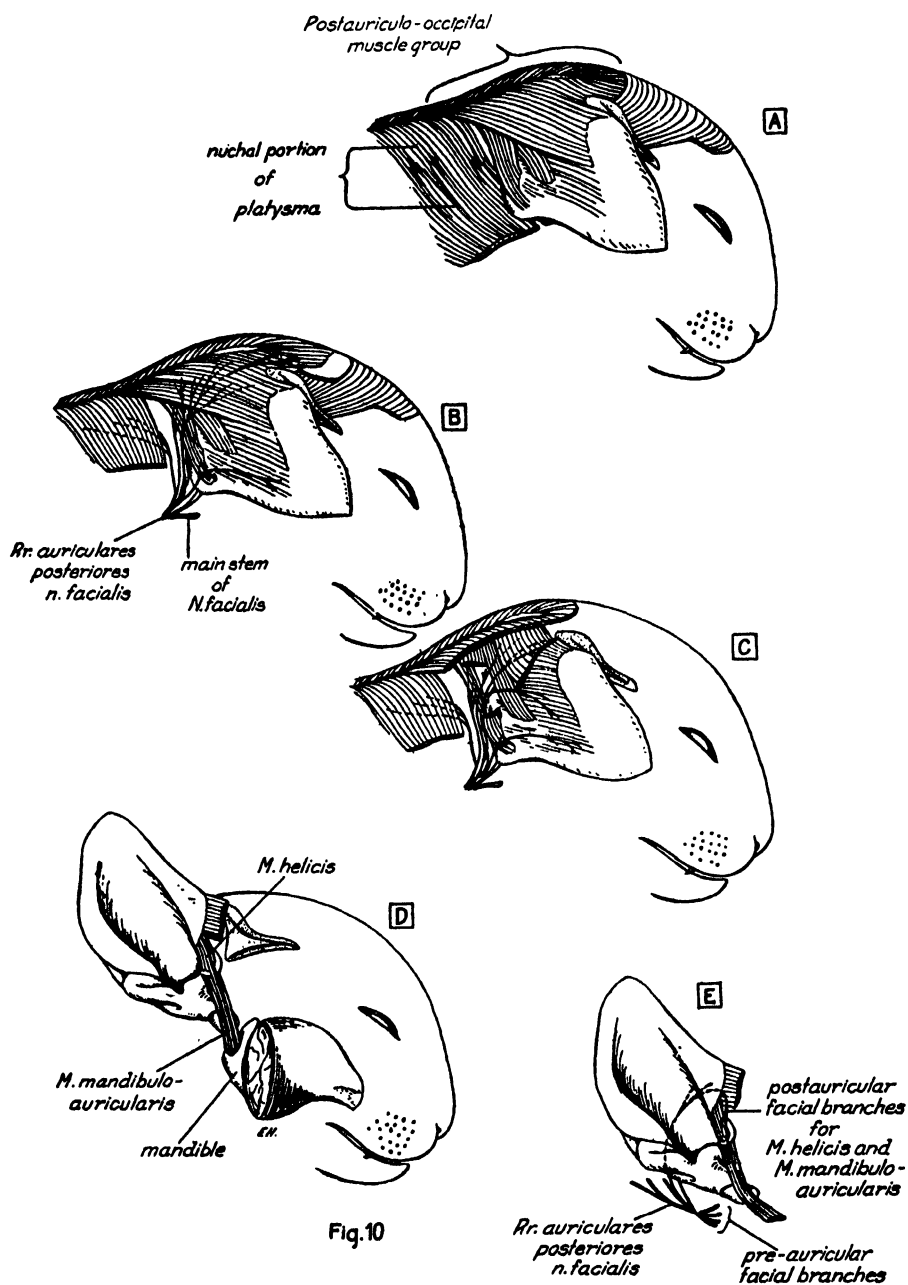


FIG. 10. CAT (CONTINUED), SHOWING THE DERIVATION OF THE POST-AURICULO-OCCIPITAL MUSCLE GROUP FROM THE NUCHAL PORTION OF THE PLATYSMA

According to this evolution we find the individual muscles of the post-auriculo-occipital muscle complex (including part of the extrinsic and intrinsic ear musculature and the *M. occipitalis* (a)) innervated by post-auricular branches of the *N. facialis*, which supply also the matrix, the nuchal portion of the platysma (figs. 10b and c).

d & e. A muscle portion in continuation with the *Mm. obliqui et transversi* has migrated from the convex surface of the ear cartilage to the anterior border of the ear (*M. belicis*) from where it proceeded in its migration along the cartilaginous ear tube as far as the mandible, thus invading the pre-auricular territory. This second muscle section forms the *M. mandibulo-auricularis*, which has become firmly attached to the mandible (fig. 10d). During the migration this muscle-tract carried its nerve supply with it. Hence the peculiar innervation of the *M. belicis* and *M. mandibulo-auricularis* through a branch of the *rami auriculares posteriores n. facialis* (fig. 10e), which passes from behind in a wide detour around the concha of the ear until it reaches these two small muscles to which it supplies terminal twigs. While in the cat primitive persisting muscle connections between the *M. mandibulo-auricularis* and the *M. belicis* (fig. 10d), and between the latter muscle and the *Mm. obliqui et transversi* on the convex surface of the ear cartilage still indicate the trail of migration, in the dog (Huber, 1922/23) these last muscle connections are lost, and the innervation through a post-auricular branch of the *N. facialis* remains the sole, though a clear, indication of the genetic origin of these muscles. This example illustrates beautifully that the nerve supply may serve as a safe guide in establishing the genetic relation of individual muscles within muscle groups (compare Huber, 1925).



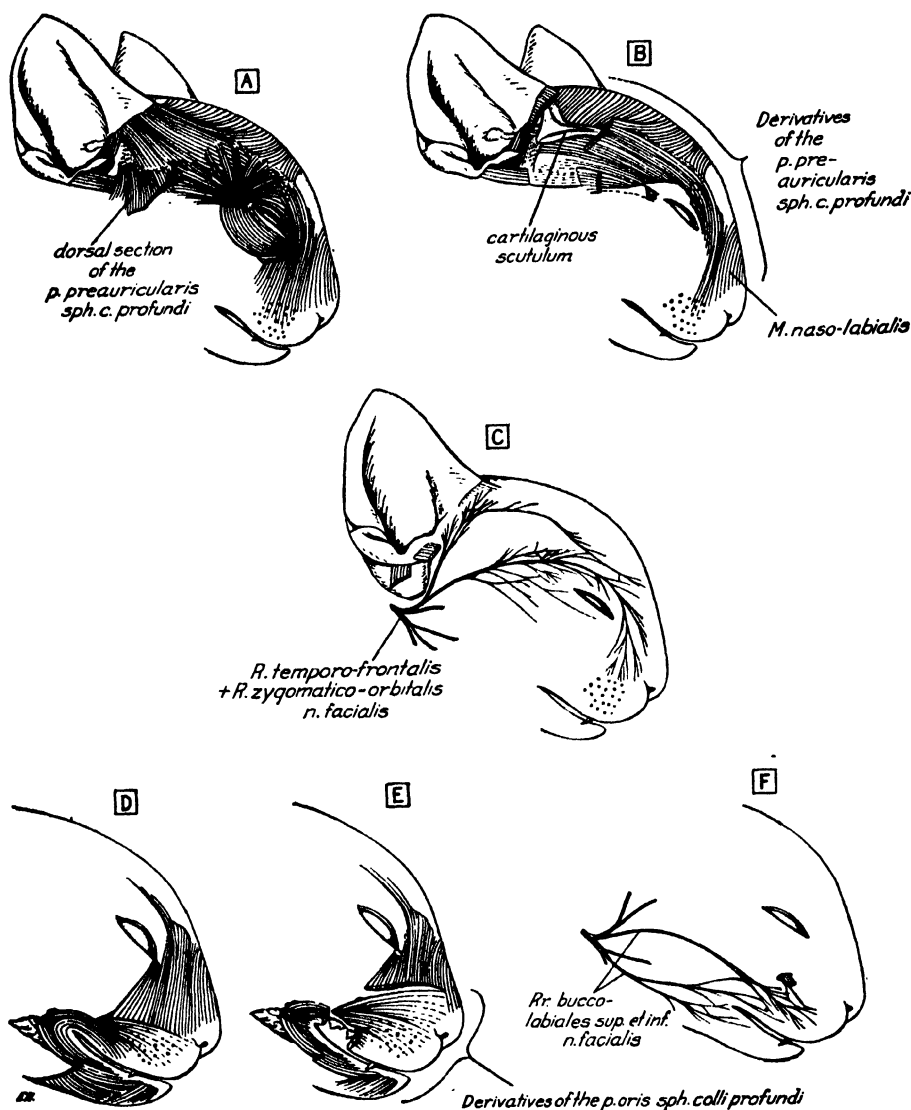


Fig.11

FIG. 11. CAT (CONTINUED), SHOWING THE MUSCLES WHICH HAVE EVOLVED FROM THE SPHINCTER COLLI PROFUNDUS

a & b. The *pars pre-auricularis* of the *sphincter colli profundus* (compare also fig. 9c) has given rise to the muscle-complex located in front of the ear and over the forehead, to the *M. orbicularis oculi*, *M. superciliaris*, *M. auriculo-labialis* (omitted in figure), and to the superficial muscle covering the lateral surface of the snout (*M. naso-labialis*). The differentiation of this musculature led to the ramification of the corresponding pre-auricular branches of the *N. facialis*, i.e., the *ramus temporo-frontalis* and the *ramus zygomatico-orbitalis* (fig. c).

d & e show the derivatives of the *pars oris*, the most anterior portion of the *sphincter colli profundus* (compare fig. 9c). These muscles (*M. orbicularis oris*, *M. buccinator*, *M. maxillo-naso-labialis* and *M. mentalis*) are innervated by the *rami bucco-labiales superior et inferior* of the *N. facialis* (fig. f). It should be mentioned that in fig. 11d the *M. naso-labialis*, which does not belong to this group (compare figs. 11a-c), is left in place simply to show the topographic relationship to the two portions of the *M. maxillo-naso-labialis*, which are separated by the *M. naso-labialis*. The innervation given in figs. 11ob, c and e; 11c and f, is based on morphological investigation (Huber, 1918, 22/23) verified by experiments (Huber, 1924; Huber and Hughson, '25).

II. CORRELATION OF THE DEVELOPMENT OF THE MOTOR NUCLEUS OF THE N. FACIALIS WITH THE EXPANSION AND DIFFERENTIATION OF THE SUPERFICIAL FACIALIS MUSCULATURE IN MAMMALS

Considering the unique expansion of the superficial facialis musculature in mammals, it is not astonishing that we find the motor component of the *nucleus n. facialis* of corresponding dimensions.

From Kappers' investigations (1910) it becomes evident that the whole facial nucleus must originally have been located close to the floor of the fourth ventricle, near the primitive taste centre. It still holds this position in some of the *lower Vertebrates* (fig. 12a). In others the facial nucleus shows the tendency to split up into two nuclei, e.g., in fishes, into a frontal and a caudal nucleus, or into a fronto-dorsal and a ventral nucleus; or, in the Sauropsida (reptiles and birds) into a dorsal and a ventral nucleus.

Although in the reptiles the facial nucleus appears to be still continuous, one can readily recognize a dorsal and a ventral portion, of about equal size (fig. 12b). The ventral portion may be found shifted ventralward away from the dorsal. This separation is more distinct in the birds (fig. 12c), where the two nuclei are quite a distance apart (compare Kappers, 1910).

From such an arrangement as found in the reptiles we can easily derive conditions as seen in the *Monotremes*. In both *Ornithorhynchus* (*Platypus*) and *Echidna* the nuclear mass of the facial, greatly increased in size as compared with that of the reptiles, is divided into two nuclei, a distinct dorsal and an equally distinct ventral nucleus (figs. 13a and b). Their expansion is frontalward into the reflex area of the motor trigeminal nucleus (Kappers, 1920, p. 533). While the dorsal nucleus remained in its primitive dorsal position, the ventral nucleus has shifted further ventralwards

than in the reptiles. However, it still holds a position midway between the floor of the fourth ventricle and the ventral surface of the brain stem (Kappers, 1910, p. 81 for *Echidna*), or (according to Koelliker, 1901, fig. 17 for *Echidna*; fig. 5 for *Ornithorhynchus*; Hines, 1929, figs. 16 and 17) slightly more ventral.

The two monotremes show some difference as to the relative size and formation of the dorsal and ventral nucleus.

In *Ornithorhynchus* the dorsal nucleus is subdivided into two portions (Hines, p. 221), while the ventral nucleus remains undivided (Koelliker, p. 36; Hines, p. 222). Koelliker (1901) and Hines (by personal communication) agree that the ventral nucleus is larger than the dorsal. According to Hines (p. 222) the dorsal nuclear mass, if projected to the surface of the floor of the 4th ventricle, has about the same antero-posterior extension as the ventral nucleus.

In *Echidna* the difference in size of the two facial nuclei is even more conspicuous than in *Ornithorhynchus*, the compact ventral nucleus being of considerably larger size than the less compact dorsal nucleus (Koelliker, Kappers). In contrast to *Ornithorhynchus* the ventral nucleus of *Echidna* is subdivided into three portions (Koelliker, p. 97). Moreover, the sagittal extension of this nucleus is peculiar (Koelliker, Kappers) in that it extends as a continuous column of large motor cells from far behind the root of the facial nerve to a great distance in front of it (Kappers, 1910). In the marsupials and placentals, on the other hand, it lies entirely behind the root of the N. *facialis*. However, the characteristic position of this nucleus in *Echidna* is not due to a shifting in a frontal direction but is merely the result of its frontal enlargement (Kappers, 1910, p. 84 footnote). The enormous size of the nuclear mass of the facial, especially in

Echidna (compare Kappers, 1920, p. 532) coincides with the development of the superficial facialis musculature in these animals (Ruge, Schulmann, Boas and Paulli, Huber). Considering the small size of the monotremes the heavy and coarse muscle bundles of their facial muscle group form a very large bulk (figs. 5, 13c and d). These muscles not only supply the area of the head but cover in heavy sheets the neck and expand caudalward into the domain of the *panniculus carnosus*. In both *Ornithorhynchus* and *Echidna* the superficial facialis musculature has gained an extensive connection with the fore limb. These latter muscle portions evidently have great functional importance. The extension and bulk of the superficial facialis musculature of *Echidna* greatly exceeds that of *Ornithorhynchus*. This is the explanation for the relatively smaller size of the facial nuclei and *N. facialis* in *Ornithorhynchus*.

While the large ventral facial nucleus of the monotremes presumably represents the motor component, there is good reason to believe that the dorsal nucleus is also motor, at least in part. In *Ornithorhynchus*, as Hines emphasizes, the cells of the dorsal nucleus appear too large and too numerous for visceral effector cells (Hines, 1929, p. 222). Moreover, the comparatively large size of the dorsal nucleus in *Ornithorhynchus* makes it very likely that many of its cells together with the cells of the ventral facial nucleus are destined for the superficial facialis musculature. However, we have no definite knowledge in regard to the functional rôle of these two nuclei (Kappers, 1920, p. 534, concerning *Echidna*; Hines, 1929, p. 222, concerning *Ornithorhynchus*). Up to this time no experimental approach towards the solution of this problem has been made.

In the *Marsupials* and *Placentals* only a very small part of the facial nucleus, mainly

of visceral nature, retains the dorsal position, while the unquestioned motor part, enormously increased in size, has shifted ventralward (fig. 14a) probably through neurobiotactic influences, nearer to the reflex tracts which bring in impulses from the mouth, nose, eyes and ears and also closer to the decussation of the facial pyramidal tracts, which transmit cortical impulses to the facial nucleus (Kappers, 1908, '10, '20/21, '27). In contrast to the monotremes this motor facial nucleus has attained a definite ventral position, lying almost directly on the base of the brain stem (Kappers, 1910, p. 84).

The phylogenetic rearrangement (ventral shifting) of the motor part of the facial nucleus in marsupials and placentals is reflected in the embryological development, whereby this nucleus shifts from a more dorsal position into its definite ventral position. During the displacement of the nucleus, the *radix n. facialis* at its emergence from the medulla oblongata evidently remains fixed, and this phenomenon leads to the peculiar formation of the facial loop, usually around the nucleus of the abducens nerve (fig. 14a).

The nuclear origin of the motor elements of the facial nerve has for a long time been subject to controversy. In order to explain the well-known fact that in cases of facial palsy of central origin in man, the mimetic muscle group supplied by the temporo-frontal and zygomatico-orbital facial branches remains unaffected, several authors have assumed a dual nuclear origin of the facial nerve. Thus it was the belief of Mendel (1887) that additional fibres to the facial arise in the nucleus of the oculomotor nerve, while Duval, Testut and others thought that the facial, as it looped over the abducens nucleus, received a contingent of fibres from it for the upper facial branches. Pure histological, as well as experimental—and clinical—his-

tological studies by a series of investigators, however, have brought conclusive evidence against a dual origin of the facial nerve. They proved that the motor part of the *nucleus facialis* is the sole source of fibres for the entire motor facial nerve.

As a result of the differentiation of the superficial *facialis* musculature and the subsequent ramification of the involved facial branches, we find subdivisions in the motor facial nucleus (fig. 14b).

A series of studies by Van Gehuchten ('93, '98), Cajal ('95), Marinesco ('98, '99), Bruce and Pirie ('08), Yagita ('10), Papez ('27), and others has been undertaken to investigate the topography of these subdivisions and to correlate them with the differentiations in the peripheral *facialis* field. In their conclusions concerning the nature of the subdivisions the various authors do not agree. The question is

whether the subdivisions of the nucleus correspond to a phylogenetic or to a functional grouping of the superficial *facialis* musculature with the corresponding peripheral facial branches involved, or whether additional factors influencing the development of the central nervous system may here play a rôle. According to the most recent publications of Papez (1927) the plan of subdivision of the facial nucleus seems to follow the phylogenetic differentiation of the superficial *facialis* musculature and the consequent branching of the facial nerve (fig. 14c) such as has been brought out through morphological investigations of the author (Huber, 1922/23; Huber and Hughson, 1926). Additional investigations on the facial nucleus of the cat undertaken by DeGaris have not come to a definite conclusion (DeGaris, *Anat. Rec.*, 1929, abstract).

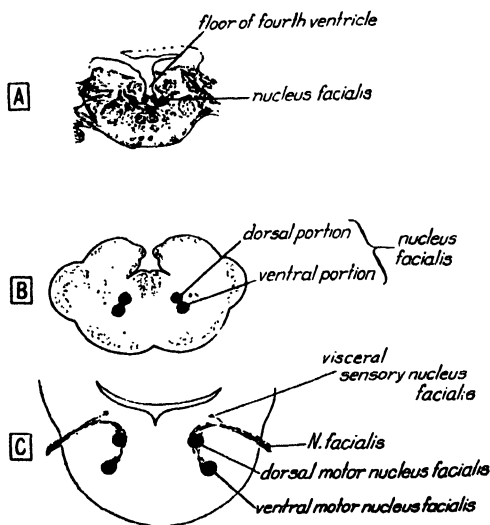


Fig. 12

FIG. 12. CROSS SECTIONS THROUGH THE MEDULLA OBLONGATA AT THE LEVEL OF THE NUCLEUS FACIALIS

a. *Gadus* (cod) as a representative of the bony fishes (after Kappers, 1910). The *nucleus facialis* is seen in a primitive dorsal position close to the floor of the 4th ventricle. Only part of this nucleus is motor, destined to supply the *facialis* musculature, which is not extensive in the fish (compare fig. 1).

b. The *facialis* nucleus in reptiles (modified after Kappers). The *nucleus facialis* has increased in size in correlation with the expansion of the superficial *facialis* musculature (compare fig. 3), and is subdivided into a dorsal and a ventral portion.

c. The *facialis* nucleus in birds (combined from Kappers, 1910, and J. Sanders, 1929). The dorsal and the ventral portion of the *nucleus facialis* are more clearly separated, thus forming two distinct nuclei.

FIG. 13. THE NUCLEAR MASS OF THE N. FACIALIS IN THE MONOTREMES, ORNITHORHYNCHUS (A) AND ECHIDNA (B), WITH ADDITIONAL FIGURES C AND D ON THE FACIAL MUSCULATURE OF ECHIDNA, TO ILLUSTRATE THE CORRELATION BETWEEN THE SIZE OF THE NUCLEUS FACIALIS AND THE BULK OF THE FACIALIS MUSCULATURE

a. The facial nuclei of *Ornithorhynchus* (after Hines, 1929).

b. The facial nuclei of *Echidna* (after Kölliker, 1901).

There are two distinct facial nuclei, the ventral having shifted further ventralwards than in the reptilian plan. In *Ornithorhynchus* the dorsal nucleus is subdivided into two portions, while the ventral nucleus remains undivided. In *Echidna* it is the dorsal nucleus which remains undivided, while the ventral nucleus shows three subdivisions. In both monotremes the ventral nucleus is found larger than the dorsal. This is more conspicuous in *Echidna*. A comparison with figure 12b shows the great increase of the nuclear mass in the monotremes,—an increase which coincides with the enormous expansion of the superficial facialis musculature in these animals (compare fig. 5 and 13c and d with fig. 3). The facial nuclei of *Echidna* (fig. b) exceed in size those of *Ornithorhynchus* (fig. a). This is in accord with the fact that in *Echidna*, the superficial facialis musculature, composed of heavy coarse muscle bundles, is more extensive and larger in bulk than that of *Ornithorhynchus*. As seen in figures 13c and d it is not confined to the region of the head and neck, but inserts into the fore limbs with several powerful portions which cover, in their origin, a considerable area of the chest (fig. c). Ventral portions (d) likewise extend caudalward into the domain of the panniculus carnosus. The arrows in figs. c & d indicate the border line between the two genetically distinct muscle territories.

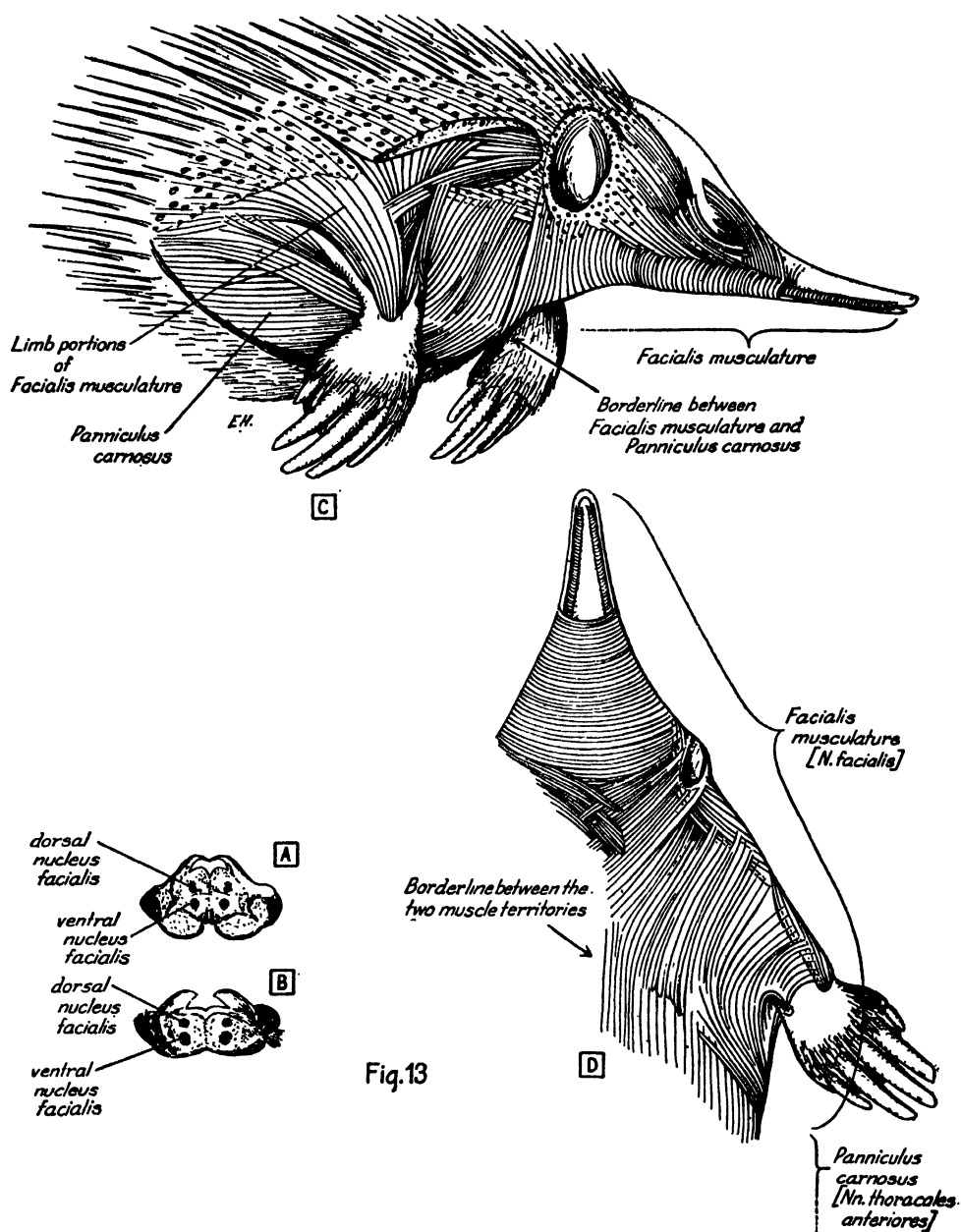


Fig.13

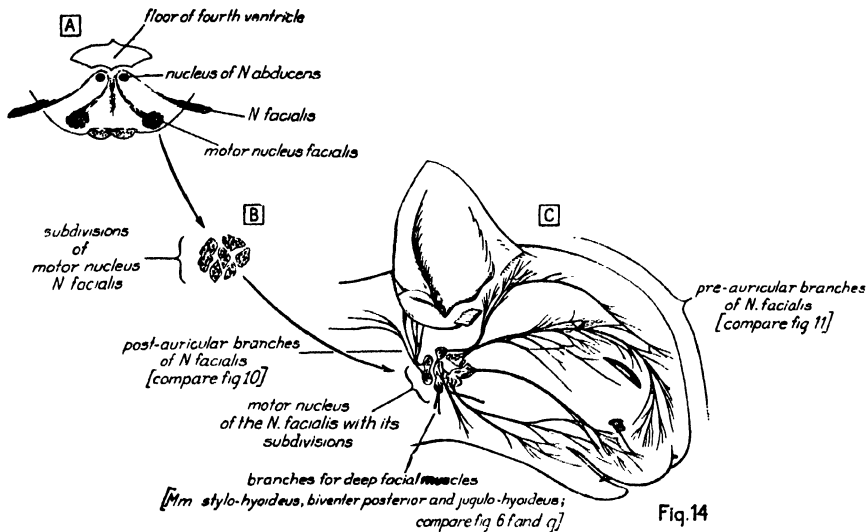


FIG. 14. THE MOTOR FACIAL NUCLEUS IN MARSUPIALS AND PLACENTALS

a. Schematic representation of a cross section through the medulla oblongata at the level of the facial nucleus, illustrating conditions characteristic of the marsupio-placentalian plan. While in the marsupials and placentals only a very small part of the facial nucleus, mainly of visceral nature, has remained in a primitive dorsal position (compare Kappers, 1910), the rest, enormously increased in size, has shifted ventralwards and is now situated almost directly on the ventral surface of the brain stem. This nuclear mass (see *a*) represents the motor facial nucleus, as evidenced through histological, experimental and clinical researches. The fibers which arise from this nucleus pass upwards, loop around the nucleus of the *N. abducens* and then turn lateralwards to form the root of the facial nerve. The size of the motor facial nucleus and facial nerve corresponds with the extension and bulk of the superficial facialis musculature.

b. Motor facial nucleus of the cat (after Papez). The cells within this nucleus are arranged in definite groups.

c. The motor facial nucleus in the cat projected on the side of the neck (figure combined from Papez, 1927, and Huber). According to Papez' investigations the subdivision of the facial motor nucleus follows the ramification of the facial nerve as determined by the phylogenetic differentiation of the facialis musculature. From the groups of motor cells of the various subdivisions of the facial nucleus arise the motor nerve fibers which build up the peripheral facial branches destined to supply the various phylogenetic groups of facial muscles, as seen in figures 6, 10 and 11.

III. LOCALIZATION OF THE FACIALIS FIELD WITHIN THE MOTOR AREA OF THE CEREBRAL CORTEX IN MONOTREMES, MARSUPIALS AND PLACENTALS

Even more important than the questions concerning the facial nucleus, is the problem of the motor localization of the facial area within the cerebral cortex.

Since the epoch making pioneer work of Fritsch and Hitzig (1870) a vast number of data from studies on the motor cortex in a number of mammalian types (monotremes, marsupials and placentals) has been accumulated. The facial area has been roughly determined in connection with the general investigations on the motor cortex. From these studies it becomes evident that the motor facial area is one of the first which, in the phylogeny of mammals, became definitely localized in the cerebral cortex.

I. Monotremes

Martin (1898/99) with great care explored the motor cortex in *Ornithorhynchus*. Movements of the facial field were obtained most easily. Stimulation of most parts of the anterior half of the cortex resulted in a "screwing-up" of the contralateral eyelids, but this movement was aroused with the weakest current at a smaller area further back (fig. 15). From the large ill-defined responsive motor area on the anterior half of the cortex Martin also obtained contraction of the anterior portion of the opposite "*panniculus carnosus*," causing the head to be rotated to the opposite side and drawing forward the shoulder. This action was evidently the result of the contraction of portions of the facialis musculature which have been erroneously included in the *panniculus carnosus* (compare Huber, 1924, p. 178 ff.).

Martin made the observation that in *Ornithorhynchus* facial and fore limb areas partly coincide, and that the hind limbs

and tail apparently have no representation in the motor cortex.

II. Marsupials

In the pouch-young opossum (*Didelphys virginiana*) Weed and Langworthy (1925) and Langworthy (1927) found that the facial area becomes responsive to electrical stimulation at a considerably later stage than the fore limb area. In view of the precedence in structural development and early use of the fore limbs, and taking in consideration some further significant points, the author concludes that this considerably earlier response from the fore limb in contrast to the response from the facial area must be due to a developmental adjustment and not, as Langworthy (1927, p. 170) suggested, to phylogenetic sequence.

In regard to the early functioning of the fore limb one should refer to Hartmann's observation that after the ten day gestation period the very immaturely born young, measuring only 11 mm. in crown-rump line, crawl without any assistance of the mother from the vaginal orifice to the pouch, where they quickly become attached to the nipples. In crawling they use the fairly well-developed fore limbs, while at this stage the hind limbs are represented merely by extensive buds. Kangaroo young reach the pouch of the mother in the same manner (C. Hartmann, 1920).

Within the facial area of the opossum (fig. 16) movements of the ear musculature, of the *M. orbicularis oculi* and of the vibrissae can be elicited. The muscle group which moves the facial vibrissae is well represented in accordance with the important functional rôle which this tactile mechanism plays in the life of the animal (see chapter VI, Huber and Smith). According to most investigators the motor facial area of polyprotodont and diprotodont marsupials partly coincides with areas from which also movements of the fore limbs are obtained. The latter appear still to have partial representation in the corpus striatum (Rogers, 1924).

As to the cortical representation of the hind limbs, the various investigators do not agree in their findings. Several authors, Herrick and Tight (1890), Ziehen (1897), Flashman (1907) and C. and O. Vogt (1906/07) reported hind limb movements, which were, however, obtained with difficulty and only through application of stronger current. Such movements when obtained were more diffuse compared with the fore limb movements. Cunningham (1897/98) and several more recent investigators (Rogers, 1923, '24; Gray and Turner, '24; Weed and Langworthy, '25; Langworthy, '27), on the other hand, were unable to obtain in the opossum movements of the hind limbs, trunk or tail, despite careful exploration of the whole cerebral cortex. Future investigations will have to give proof whether there possibly occur progressive individual variations, in which part of the motor center for the hind limbs has shifted into the cortex. This seems a possible explanation for the positive results of the first group of investigators.

III. Placentals

There are a series of orders and suborders of the placentals which have never been subjected to experimentation, while of the others only one or a few representatives have been studied.

1. *Insectivores*. Of this order, only the hedgehog (*Erinaceus europaeus*) has been investigated. The results obtained by the various investigators differ widely. They are in part uncertain, and incomplete. For example, Mann (1896) failed to obtain response from any part of the facialis musculature, while Ziehen (1897) and C. and O. Vogt (1906/07) observed no movements of the *M. orbicularis oculi* nor of the ear musculature. Evidently those facial muscles which during the life of the insectivores, play the greatest rôle (i.e. the

muscles of the snout) are the best represented (Ziehen; Probst, 1901; C. and O. Vogt), while the other muscles of the facialis group do not readily respond (see Ziehen, '99, p. 169, in contrast to '97). The snout musculature appears to be bilaterally represented (C. and O. Vogt).

Besides the facial area, areas for the fore and also for the hind limbs have been located. The movements hereby elicited were isolated, uncorrelated movements of certain muscle groups only, and not easily obtained.

2. *Bats*. C. and O. Vogt (1906/07) found in the fruit bat (*Pteropus*) the "head segment" with the facial area far more extensive and more responsive than the leg areas. Various subdivisions of the facial area were mapped out, which responded with three different kinds of "rhythmic movements" of the muscles of the snout, *M. orbicularis oculi* and ear musculature.

3. "*Rodents*," (including the rodents in the strict sense, and the lagomorph or duplicitent rodents). The investigations on the motor cortex of mouse, rat, rabbit, guinea-pig and some further rodents by various authors (Ferrier, 1873, '74, '80/86; Fürstner, '76; v. Bechterew, 1886/87, '87, '11; Exner and Paneth, '87; Herrick and Tight, '90; Mann, '96; Mills, '96; Ziehen, '97; Simpson, 1914, '15; Lashley, '21; W. K. Smith, unpublished) show that the motor cortex of the rodents is ill-defined and variable. It is still on a very primitive evolutionary level (compare Herrick, 1926, p. 165). The data so far obtained, however, are very incomplete, in part contradictory and as yet little correlated.

Interesting are the results of stimulation experiments on new-born and very young rabbits in comparison with new-born and near-term fetuses of guinea-pigs. In the rabbit Tarchanoff (1878) did not obtain

any movements until the animals were about eleven days old. Then it was possible to elicit fore limb and masticatory movements. Only considerably later were movements of the hind limbs obtained. According to Tarchanoff (p. 860/861) the area for masticatory movements, in which also the orbicularis oris-buccinator group of the facialis musculature is involved, is in the young rabbit more responsive than the fore limb area, whereas the hind limb area did not give regular response. While Tarchanoff and several subsequent authors claim in the rabbit a responsive hind limb area, besides the areas for the fore limb, facial and masticatory musculature, Mills ('96), after examination of a large series of different breeds of young and adult rabbits, emphatically denies the existence of a responsive hind limb area in this animal. Mills found the rabbit in striking contrast with the guinea-pig, rat and mouse. In these latter rodents he could confirm the general motor localization such as previously found by Ferrier, who located a hind limb area in addition to the other areas (compare Mills, p. 28). Most significant is the fact that in the rabbit (compare v. Lenhossék, 1889; Simpson, '14, '15) as in a series of further rodents (compare v. Lenhossék, '89; Goldstein, 1903/04; Wallenberg, '03/04; van der Vloet, '06; King, '10; Simpson, '12/13, '14, '15; Ranson, '13, '14; Linowiecki, '14; Reveley, '15) the cortico-spinal tract could be traced, though greatly reduced at least as far as the lumbar part of the spinal cord. In some cases this tract extended even to the sacral sections of the cord. Thus there evidently exists in these "rodents," including the rabbit, a definite anatomical basis for positive cortical motor response of the hind limbs.

Motor response is obtained in the guinea-pig much earlier than in the rabbit,

occurring at birth or within a few hours after birth (Tarchanoff, 1878; Langlois, '89; Mills, '96), or even shortly before birth (Tarchanoff). In new-born guinea-pigs Tarchanoff and Langlois obtained movements of mastication, fore limb movements, and (with stronger current: Langlois) also movements of the hind limbs. By far the easiest to obtain were the masticatory movements (Tarchanoff, Langlois, Mills), in which, presumably besides the masticatory musculature, the orbicularis oris-buccinator group of the facialis musculature are involved just as in the rabbit.

The great difference in first appearance of motor responses in the guinea-pig compared with the rabbit, rat and mouse is undoubtedly correlated with the difference in the state of general development in which these rodents are born. While rabbits, rats, and mice are born in a very immature and helpless state, the guinea-pigs come into the world in a relatively mature condition with a well developed coat of fur and with open eyes, able to run around. Von Lenhossék (1889) also emphasizes the fact that in the new-born guinea-pig the tracts of the spinal cord, including the pyramidal system, are further advanced in development and larger in size than in the new-born rabbit or mouse.

It is noteworthy that in both rabbit and guinea-pig the masticatory movements prevail over the movements of the fore limbs. This is in striking contrast to results obtained in the opossum (referred to above), cat and dog (see later). It is very likely that in the various mammalian types developmental adjustments of the various motor centers take place according to the differences in behavior during early postnatal life (compare also Mills' extensive studies on the psychic development of various types of placentals, 1894, '95, '96).

4. *Ungulates.* The motor cortex of the sheep and goat as representatives of this

order have been studied by Marcacci (1877), Ziehen ('99), Dexler and Margulies (1906), Simpson and King ('11), Bianchi ('20), Bagley ('22), and W. K. Smith (unpublished). The results obtained by the various investigators are in part contradictory and indefinite. A series of responsive areas which show considerable individual differences have been mapped out. Among these is a facial area, which gives response of the contralateral and in part bilateral facialis musculature. Besides the main facial area Bagley located an additional well defined area which readily responded with homolateral contractions of facial muscles of the mouth. In agreement with Marcacci and in contrast to Simpson and King, Bagley found the facial area more responsive than the other areas. According to most authors, response from the fore legs is more easily obtained than from the hind legs. Marcacci was unable to obtain movements from the latter.

5. *Carnivores*. Of special interest are the developmental studies on the motor cortex of cat and dog. Because of the divergence in reported results the findings on these two animals will now be given separately.

The cortex of *cats* at birth and for several days after did not respond to electrical stimulation according to Mills (1896), but in some cases the cortex was functionally active before the eyes opened, i.e., before the ninth day. The centers for the fore limbs were found responsive earlier than those for the hind limbs, and head movements could be obtained only at a later date than movements of the limbs.

Among the subsequent investigators Weed and Langworthy ('1926), and Langworthy ('27) obtained fore limb movements in kittens at birth (fig. 17a), while, strangely enough, hind limb movements could not be obtained until the kittens

were sixteen days old, and the "facial area" did not respond to electrical stimulation until twenty-one days of age. The animals were, as in Mills' experiments, stimulated under ether anesthesia, which the investigators considered essential in order to exclude the possibility of spontaneous movements being interpreted as due to the results of electrical excitation (Weed and Langworthy, p. 95).

Soltmann (1876), who deserves credit for having initiated these studies on the motor cortex of new-born and very young animals, came to the conclusion that the development of function of the motor cortex is determined by the time of opening of the eye slit.

In *dogs*, Soltmann found the motor cortex not responsive until the tenth day after birth, when the first fore limb movements were obtained. At the thirteenth day, movements of the hind limbs together with fore limb movements could be elicited. But it was not until the sixteenth day that movements from the facial area were obtained. Soltmann used in his experiments on puppies ether or chloroform as anesthetics or gave subcutaneous injections of morphia.

Later, Ferrier (1880/86) agreed that in puppies no limb movements are obtained until after the opening of the eyes, usually about the eighth day, stating that generally the cortical centers in the dog do not react till about the tenth day, and that the centers of the fore limbs become excitable before those of the hind limbs.

Mills ('96) also came to the conclusion (p. 9) that there is no proper functional cortical development in dogs before the eyes open, which seldom occurs before the tenth to the thirteenth day (p. 17). He confirmed Soltmann in that the movements of the head as a whole and of its various parts are developed later than those of the limbs. However, in disagreement with

Soltmann and Ferrier he found that in most, though not in all of his cases the hind leg was functionally active at a somewhat earlier date than the fore limb,—an observation which could not be confirmed by subsequent investigators. In the case of large dogs, as the St. Bernard, the cortical motor centers became functionally active at a later date than in small breeds, like the "terriers" or in mongrels, an important observation which seems in harmony with the more rapid physical and psychic development of the latter (p. 9, 10, 21). In agreement with Soltmann, Mills (p. 16) emphasizes that the localization at first is somewhat indefinite, but gradually, though rapidly, becomes better defined. He found the principal centers active within the first thirty days of life; most of them earlier (p. 10). Mills, like his fore-runner, stimulated his puppies under anesthesia using ether.

Paneth (1885), however, using no anesthesia, obtained positive results in dogs within 24 to 48 hours after birth. These puppies responded to electrical stimuli prevailing with fore limb movements, while hind limb movements were sparingly obtained.

Subsequent investigators, Michailow (1910) and v. Bechterew (1911), in dogs, likewise obtained positive results during the first few days of postnatal life. They were able at this time to locate electrically excitable areas for both fore and hind limbs, for mastication and for neck movements. The facial area became responsive considerably later, not until five days after birth, when closure of the eyes, and ear movements were obtained. Several days later the authors obtained in addition, movements of the upper lip. In agreement with Soltmann ('76) and Mills ('94, '95, '96) they found considerable individual variability as well as variability according to the different breeds of dogs.

Cat and dog as seen from the experiments of the various investigators exhibit the striking phenomenon that the limb areas considerably precede the facial area in their response to electrical stimulation, and that (according to Soltmann, Ferrier, Paneth, Michailow, v. Bechterew, Weed and Langworthy) the fore limb area precedes the hind limb area. Comparison with conditions found in the adult monotremes, marsupials and primitive representatives of the placentals moreover evidences the fact that, as regards the cortical motor representation, the fore limbs, presumably in functional adaptation, precede the hind limbs not only in the development of the individual but likewise in phylogeny. However, the great delay in the response from the hind limb and facial areas in the cat (Weed and Langworthy) as compared with the dog, is rather astonishing in view of the fact that cats in their general development during postnatal life make quicker progress than dogs (compare Mills on the psychic development of young animals, 1895, '96, p. 21). Renewed investigations with modification of the technique (e.g., stimulation of the animals without anesthesia) may yet lessen the unaccounted great difference between cats and dogs.

From the investigations by Fritsch and Hitzig (1870), Ferrier ('73, '74, '80, '86), Hitzig ('73, '74, '04), Luciani and Tamburini ('78, '83), Rosenbach and Bechterew ('83), Paneth ('85), Bechterew ('86/87, '87, 1911), Exner and Paneth ('87), Herrick and Tight ('90), Mann ('96), Mills ('96), Weed and Langworthy ('26), Langworthy ('27), etc. and from our own (Huber and Smith, unpublished) it becomes evident that the motor cortex in carnivores, especially cat and dog, has evolved further than in representatives of the above discussed orders of placentals. The readily responsive facial area appears to be more clearly

separated from the fore limb area (fig. 17b). Contraction of the facialis musculature is prevaillingly contralateral, but to a certain extent also bilateral. Within the facial area, those muscles (fig. 11) which move the long mystacial tactile vibrissae (*M. naso-labialis* and *M. maxillo-naso-labialis*) are the most responsive ones, especially in the cat (see further chapter VI). Portions of the *M. orbicularis oculi* contract synergetically with the *M. naso-labialis*. The two muscles constitute a morphological and functional unit, and the cortical center for this genetic muscle group has evidently not received a further clear subdivision.

6. *Primates*. A far greater variety of the Primates has been investigated than of any other order of the placentals. It was, indeed, of great importance that these investigations should cover the main groups of the Primates in order, on the one hand, to link the findings in the lower representatives of this order with those of primitive types of other placentalian orders, and, on the other hand, to get, through comparative study of the catarrhine monkeys and apes, a key for the understanding of the complex conditions of the human motor cortex.

While many important general questions on the primate motor cortex have been intensively studied by a large series of investigators, our knowledge concerning the representation of the facial area in the motor cortex of the primates is very incomplete and in part contradictory. It is not at all correlated with the data from the extensive studies on the facialis musculature of this order (chapter VII).

A. Prosimiae (Tarsioidea and Lemuroidea).

Tarsius has not yet been subjected to experimentation, but there are records of observations on a number of the *Lemuroidea* by Elliot Smith and May (1904), Völsch ('06), C. Vogt ('06), C. and O.

Vogt (1906/07) and Mott and Halliburton ('08).

In the brain of the Lemuroidea (fig. 18a) distinct responsive areas for the head, trunk, tail and both extremities were mapped out. From the facial area, movements of the *M. orbicularis oculi* and the musculature of the ears and snout were obtained. None of the investigators referred to vibrissae movements, which in the lemur should be expected to be an outstanding phenomenon (compare chapter VII). Easily obtainable contralateral ear movements were reported (C. and O. Vogt; Mott and Halliburton). This is in agreement with the fact that in the lemurs the ear musculature is well developed and differentiated (Ruge, Huber) corresponding to the great rôle which hearing, with the necessary adjusting mechanisms of the outer ear, plays in the nocturnal life of the animals. The closure of the eye was found prevaillingly contralateral, while the snout musculature gave contralateral and bilateral response (C. and O. Vogt, p. 404). The Vogts emphasize the more caudal position of the area for closure of the eyes as being in striking contrast to the more oral position of the same area in the Simian cortex (p. 397, 406).

B. Simiae:

1. *Platyrrhines.*

a) *Family Hapalidae (Marmosets)*. Investigations on representatives of this family were undertaken by C. and O. Vogt (1906/07), and Mott, Schuster and Halliburton (1910).

In agreement with the lowly position of the marmosets, their little or unfurrowed brain has no *sulcus centralis* which in the higher simians demarcates so clearly the motor area in front from the sensory area behind. However, the responsive motor cortex (fig. 18b) shows a topographic relation similar to that in the monkeys with a well defined *sulcus*

centralis Rolandi (figs. 18c—e). Responsive areas for the trunk, tail, upper and lower extremities and head have been mapped out. Mott, Schuster and Halliburton emphasize the large extension of the head area, including the facial field, which could be further subdivided and gave a more ready response than the fore and hind leg areas. In contrast to their previous investigation on the lemur (Mott and Halliburton, 1908) the authors did not obtain response from the ear musculature in the marmoset. Neither did C. and O. Vogt record ear movements. However, this negative result must not be considered final. It should rather be expected that a more elaborate investigation of the facial area will give ear movements, since the marmosets possess a well developed and fully functioning, though not highly differentiated ear musculature (chapter VII).

b) *Family Cebidae*. C. and O. Vogt (1906/07) seem to be the only authors who have experimented on representatives of this family—on *Nyctipithecus* (*Aotus*), *Pithecia*, *Cebus*, *Alouatta* and *Ateles* (fig. 18c). These important investigations of the Vogts bring, however, only scanty contributions to the exact knowledge of the facial area. It should be expected that a further elaboration of this area would take place in the "ascending scale of platyrrhines," paralleling the evolution of the *facialis* musculature. In the higher platyrrhines the fuller use of the more elaborate muscles of the face proper (mimetic musculature) is in striking contrast with the prevailing use of the musculature of the ear and snout and the specialized vibrissae moving facial muscles in the lower platyrrhines and prosimians (chapter VII).

2. *Catarrhines*. The number of the investigators who have carried out stimulation and ablation experiments and his-

tological studies on the motor cortex of catarrhines is large. Since the problems hereby involved become more manifold and more complex in the "ascending scale of the catarrhines" the widely scattered literature on this subject has grown very extensive. The author has dealt more fully with this literature in another paper *A Phylogenetic Aspect of the Motor Cortex and the Cortico-Spinal Tract in Mammals, with Emphasis on the Facial Area* (in manuscript), while here only brief reference is made to it.

a) *Lower Catarrhine Monkeys* (*Cercopithecidae*). Hitzig (1874) was largely correct in his findings after exploration and delineation of the motor cortex of his only macaque. He clearly demonstrated and emphasized the fact that the electrically responsive area does not extend behind the *sulcus centralis Rolandi*. Ferrier (1874, '75, '80/86) claimed a much more extensive area including the postcentral gyrus, with additional areas scattered all over the outer surface of the cortex and even an area on the lower surface of the temporal lobe. A series of investigators (Horsley and Schäfer, 1884, '89; Schäfer, '87; Beevor and Horsley, '87, '94; Munk, '90, '92, '96, '03; v. Bechterew, '98, '99; Probst, '03; Rothmann, '04, '05, '07; E. Weber, 1906, and others) subsequently investigated the motor cortex of lower catarrhines. Partly influenced by Ferrier's inaccurate findings these authors mapped out the motor area in an extension far greater than actually exists, always including the postcentral gyrus in the electrically responsive area.

Then followed important contributions by various investigators (Sherrington and Grünbaum, 1901/02, '04; Brodmann, 1904, '05; O. Vogt, '06; Sherrington, '06; Sherrington and Roaf, '06; C. and O. Vogt, '06/07; Jolly and Simpson, '07), which indirectly (Sherrington and Grünbaum, '01/02, '04) or directly led to a more correct

delimitation of the motor areas in the lower catarrhines.

Yet for a long time it was disputed whether the postcentral gyrus had to be included in the electrically excitable motor cortex (compare controversies between Lewandowsky and Simons, 1909, '13, against Rothmann, '04, '05, '07, '12). As regards the precentral gyrus of the lower catarrhines (fig. 18d), the numerous experiments by many investigators including ourselves (Huber and Smith: on the macaque), agree in that response is readily and consistently obtained and the movements elicited are quite elaborate though not as elaborate as found in the anthropoid apes.

b) Gibbons (Hylobates and Symphalangus).

C. and O. Vogt (1906/07), shortly refer to a stimulation experiment on *Symphalangus* by Brodmann. A fuller experimental and histological investigation on a second gibbon was made by Mott, Schuster and Sherrington (1911). In contrast to the lower catarrhines, the head area in the gibbon appeared relatively small in comparison with the extremity areas. Among these the arm area showed a striking increase in size, obviously in correlation with the deliberate use of the upper extremities in the brachiating habits of the gibbon.

c) Great Anthropoid Apes (Orang-Utan, Chimpanzee and Gorilla). It was not until 1891 that for the first time a representative of the great anthropoid apes, an orang, was subjected to experimentation by Beevor and Horsley. This was a step further in the study of the primate cortex and towards our knowledge of the motor functions of the human brain. This study was followed by the extensive stimulation and ablation experiments by Sherrington and his co-workers (Grünbaum and Sherrington, 1901/02, '04; Roaf and Sherrington, '06; Brown and Sherrington, '12, '13;

Brown, '14; Leyton and Sherrington, '17). The last publication sums up the results and draws the conclusions from experiments on 3 orangs, 22 chimpanzees and 3 gorillas. An additional short account of the stimulation of an orang is included in C. and O. Vogt's work (1906/07).

The motor area of the anthropoid brain (fig. 18e), as compared with that of the gibbon and the lower catarrhines, was found to have grown in absolute extent, while other areas belonging to the so-called "silent" fields have increased still more. This vast expansion of unexcitable, richly convoluted fields is indeed among the most outstanding features of the highly organized neo-pallium of the anthropoid brain. Within the excitable motor area of the anthropoid brain, the areas representing the various parts of the body are arranged as in the lower catarrhines and higher platyrrhines. However, according to all investigators, more elaborate and very numerous movements from small subdivisions of the motor cortex can be obtained in the anthropoid brain. Thus we see in the "ascending scale of the primates" that the motor cortex evolves by individualization of emerging smaller areas within the principal motor area.

The three great anthropoid apes seem to resemble each other closely in regard to the motor cortex. But there are great individual variations and differences in the smaller details of localization of the right and left motor cortex of the same animal. In the orang, the facial area was found more extensive in relation to the rest of the motor area, being considerably longer from above down than in the chimpanzee and gorilla (Sherrington, 1906, p. 276; Leyton and Sherrington, 1917, p. 219). But apart from this distinction, there seemed no clear difference between the

motor area of the three types of the big anthropoid apes (Leyton and Sherrington, 1917, p. 219). That the motor cortex of the orang would differ, at least to some extent, from that of the chimpanzee and the gorilla could be expected in view of the fact that in the other organ systems the orangutan departs widely from his anthropoid cousins, the chimpanzee and gorilla, who stay closely together. This has been found most striking in a close comparison of the mimetic musculature of the three types (Ruge, 1887; Huber, see figures of chapter VII). Renewed, comparative studies on the motor cortex of the three great anthropoid apes may possibly bring out further differences.

The comparative anatomical investigations on the catarrhine monkeys and the apes were of great significance in regard to the cortical representation of the mimetic musculature of man. In catarrhine monkeys and also in anthropoid apes, the mimetic musculature not only of the upper but also of the lower part of the face, especially of the lips, has been reported to be in part bilaterally represented in the motor cortex (compare e. g., Beever and Horsley, 1894, on the macaque; 1891, on the orang). Such bilateral movements of the lip musculature in the orang have not been confirmed by the subsequent investigators. Contrary to Beever and Horsley, Sherrington and his co-workers found that in the anthropoid apes bilateral representation of the mimetic musculature is restricted to and even accentuated in the muscles of the upper region of the face, i. e., the *M. orbicularis oculi*, *Mm. depressor* and *corrugator supercilii* and *M. frontalis*,

but most noticeably in the *M. orbicularis oculi* (Grünbaum and Sherrington, 1904; Leyton and Sherrington, 1917). In this respect the great anthropoid apes thus resemble man closely, in whom, as seen from clinical cases and physiological observations, the mimetic muscles of the upper part of the face are evidently bilaterally represented.

d) *Man*. In order to make the study of the primate motor cortex complete, systematic experimental investigations on the motor cortex of man (fig. 19), in addition to the occasional clinical observations and the numerous data from brain pathology, were a prerequisite. Fortunately such data have been obtained through the efforts of a series of surgeons and neurologists (Krause, 1904, '05; Mills and Frazier, 1905; Cushing, '09; van Valkenburg, '12, *et alii*). For obvious reasons these experimental data from man cannot be as complete as those made during experiments on animals. Important is the fact that the results so far obtained, including those regarding the facial area, closely correspond with the results from the numerous and manifold experiments on the big anthropoid apes. This is in accord with the studies on the cyto-architecture of the anthropoid and the human cortex (Campbell, 1905; Brodmann, '09; v. Economo and Koskinas, '25).

In conclusion to this chapter the author suggests that special investigations on the facial area of the motor cortex should be undertaken with a broad knowledge of the facialis musculature with its manifold development and functional differentiation in the various mammalian groups.

FIG. 15. THE BRAIN OF ORNITHORHYNCHUS, WITH THE ELECTRICALLY RESPONSIVE MOTOR AREAS MAPPED OUT ON THE UNFURROWED CEREBRAL CORTEX

(According to experiments by Martin (1898/99).) Already in this archaic mammal the facialis field appears to be well represented in the motor cortex. From a large ill-defined area on the anterior half of the cortex, movements of the facialis musculature and of the fore limbs were obtained. Here facial and fore limb areas coincide in part, while a smaller area further back gave response of the facialis musculature only. No response of the hind limbs or tail was obtained.

FIG. 16. THE FORE BRAIN OF DIDELPHYS MARSUPIALIS (OPOSSUM) TO SHOW THE RELATION OF THE FACIAL AREA TO THE OTHER ELECTRICALLY RESPONSIVE AREAS OF THE CEREBRAL MOTOR CORTEX (MODIFIED AFTER WEED AND LANGWORTHY, 1925, AND FURTHER AUTHORS)

The main electrically responsive areas are grouped around the orbital sulcus. There facial and fore-limb areas overlap in part. Stimulation of the facial area at the lower end of the orbital sulcus also produces response of those facial muscles which move the facial tactile vibrissae (compare Huber and Smith), an outstanding phenomenon in stimulation of the opossum's cortex. Some investigators moreover reported hind limb and tail movements upon electrical stimulation of areas situated posterior to the fore-limb area. This response is, however, not regularly obtained, and has been disputed by more recent investigators.

(Note that facial and masticatory areas are closely associated.)

FIG. 17. THE FORE BRAIN OF THE CAT WITH THE ELECTRICALLY RESPONSIVE AREAS

a. New-born kitten (after Weed and Langworthy, 1926). The only response obtained at this age is from the fore limb area, which is situated in the same location as in the adult cat.

b. Adult cat (after Weed and Langworthy, and after observations by Huber and Smith). The electrically responsive areas are grouped around the *sulcus cruciatus*. From the well defined facial area at the lower end of this sulcus also movements of the facial tactile vibrissae, particularly of the mystacial vibrissae, are easily and regularly obtained. These movements are effected by contraction of the *M. naso-labialis* and *M. maxillo-naso-labialis*, as evidenced by exposing these muscles during the stimulation experiments (Huber and Smith).

(Note that facial and masticatory areas are closely associated.)

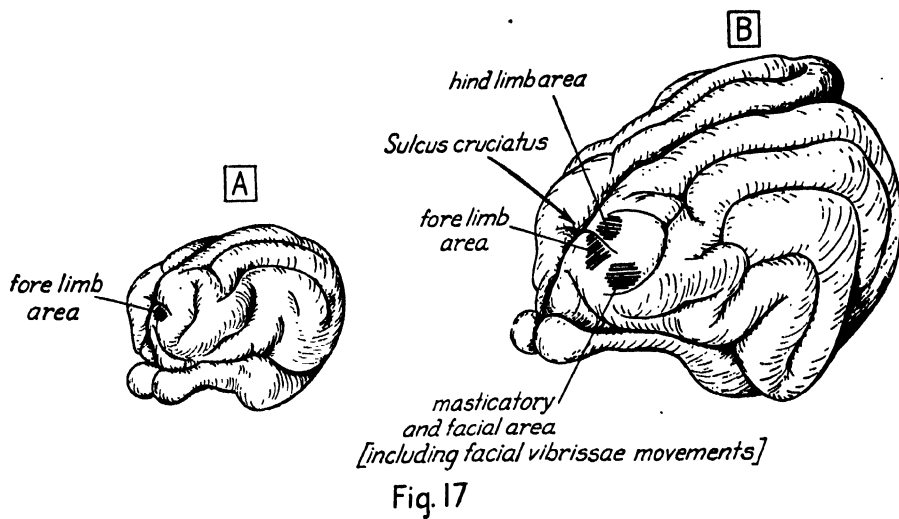
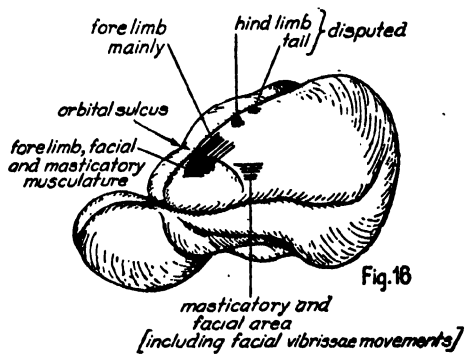
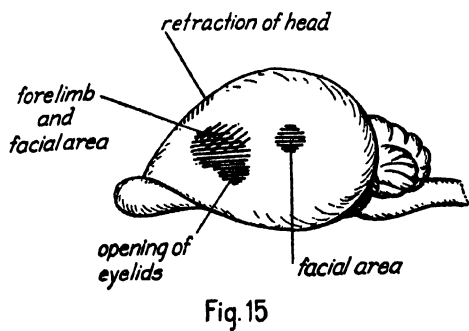


FIG. 18. THE FORE BRAIN OF SOME SELECTED TYPES IN THE "ASCENDING SCALE" OF THE PRIMATES, SHOWING THE FACIAL AREA IN RELATION TO THE OTHER ELECTRICALLY RESPONSIVE AREAS ON THE LATERAL SURFACE OF THE CEREBRAL CORTEX

The motor field in the primates is a strip anterior to the *sulcus centralis Rolandi*, which separates it from the sensory field behind. Dorsally the motor area extends over on the medial surface of the hemisphere, and in the primates with a convoluted cortex it dips into the corresponding sulci. This increase of the motor field is very considerable in the richly convoluted cortex of the higher primates (compare *e*). The facial area is part of the "head area," which is situated at the lower end of the motor field. In addition to the facial area the "head area" includes subdivisions representing the masticatory muscles, the musculature of the tongue, larynx and vocal cord. Facial and masticatory areas are closely associated.

a. Lemur as a representative of the Prosimians (after C. and O. Vogt, 1906/07). The short furrow foreground showing the *sulcus centralis Rolandi* demarcates the motor area in front from the sensory area behind.

b. *Callithrix* (marmoset) representing the lower platyrrhine monkeys (after C. and O. Vogt). In the unfurrowed brain of the Hapalidae the electrically responsive motor field shows the same topographic relations as in the monkeys which possess a well defined *sulcus centralis Rolandi*. This fact, together with the findings in various types of the Prosimians, in full agreement with the histological findings of Brodmann (1909) and others, proves that in the phylogeny of the primate cortex the cyto-architecture precedes the formation of the sulci and gyri.

c. *Ateles* (spider monkey) representing the higher platyrrhines (after C. and O. Vogt). There is a well defined *sulcus centralis Rolandi*, which marks the posterior border of the motor cortex. More elaborate movements of the prehensile tactile tail, of the hand and fingers obtained from more extensive areas in the spider monkey suggest a close correlation of morphological and physiological features of the motor areas with the habits of this splendidly adapted arboreal primate type. Only scanty contributions have been made towards the exploration of the facial area.

d. Macaque (combined from stimulation experiments by various authors, including Huber and Smith). Response from the motor field, including the facial area, is readily and consistently obtained, and the movements are quite elaborate, though not as elaborate as found in the anthropoid apes.

e. Chimpanzee (after Grünbaum and Sherrington, 1901/02, with further elaboration of the motor field, including the facial area.

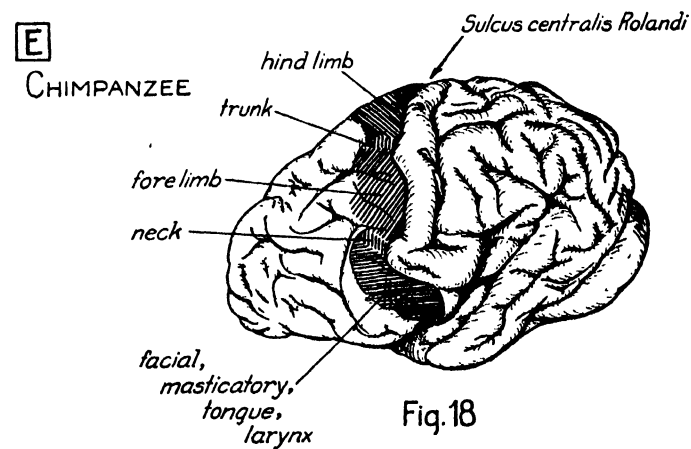
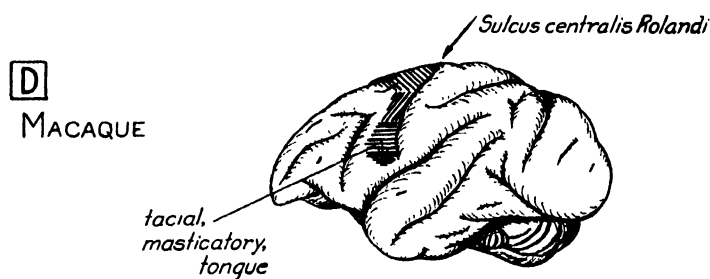
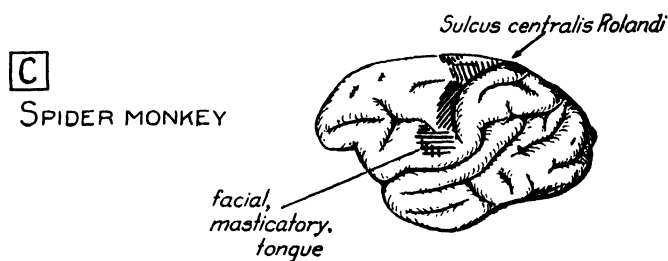
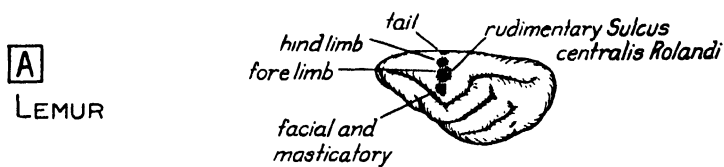


Fig. 18

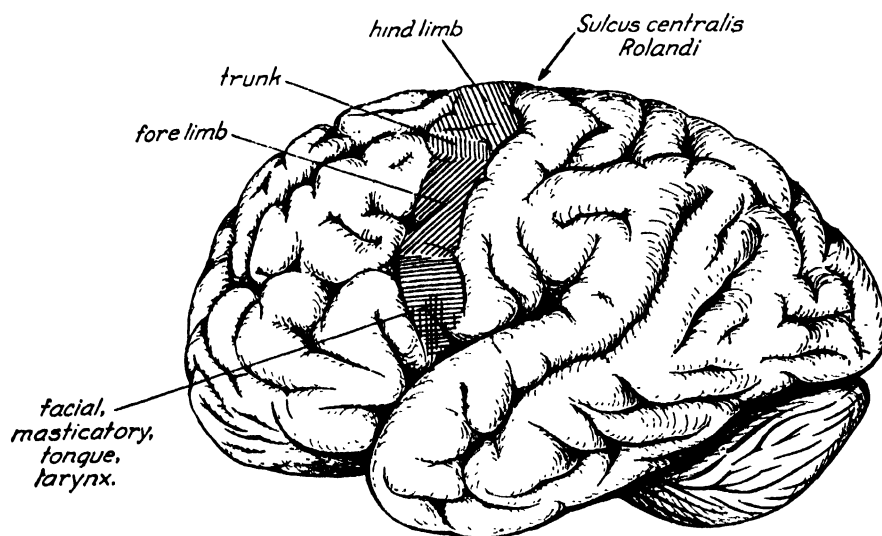


Fig.19

FIG. 19. THE FORE BRAIN OF MAN (OUTLINE FROM SPALTERHOLZ' ATLAS WITH THE FINDINGS FROM STIMULATION EXPERIMENTS BY KRAUSE, MILLS AND FRAZIER, CUSHING, VAN VALKENBURG, ET ALII)

The arrangement of the motor field including the facial area on the highly convoluted cortex closely corresponds with that of the anthropoid apes (compare fig. 18c).

IV. DECLINE OF THE SENSORY FACIAL FIELD
IN THE ASCENDING SCALE OF VERTEBRATES,
WITH VESTIGIAL CUTANEOUS AREA IN
MAMMALS. THE RISE OF THE CUTANEOUS
FIELD OF THE N. TRIGEMINUS IN THE
MAMMALS

The high development and manifold specialization of the motor facialis field of the mammals remains in striking contrast to the limited sensory field of the *N. facialis*.

In the *aquatic lower vertebrates* (fishes, aquatic amphibians and larval, branchial stages of the land amphibians) the sensory component of the *N. facialis* is of very considerable size, especially on account of the supply to the lateral-line organs, while in the adult *land amphibians* it is considerably reduced through the complete loss of these organs. In such a reduced state the sensory field of the *N. facialis* persists in the *reptiles*. In the *birds* it has undergone even further reduction (compare Kappers, 1910).

The reduced state of the sensory facialis field was taken over by the *mammals* from the reptilian ground plan. In mammals, including the primates with man, the facial sensory area is restricted to the inner ear, middle ear, the *cellulae mastoideae*, and the outer ear including the ear tube and the convex surface of the auricle (compare Boas, 1912; Huber, 1922/23, p. 376, and 1925, figs., and others), as well as to a variable adjacent skin area (see also Donath, 1906; Hunt, '07, '09, '15; Mills, '10; Clark and Taylor, '10; Kidd, '14; H. T. Davis, '14; L. E. Davis, '23; Reinhart '19, *et alii*). Moreover, it supplies the region of the fauces and the anterior two-thirds of the tongue, where the special sensory components innervate the taste buds on the *papillae fungiformes*.

Insignificant as the sensory component of the *N. facialis* in man may appear, it has its clinical importance through neuralgic

affections of the internal, middle and external ear, at times combined with trophic disturbances of the auricle and its surroundings causing Herpes oticus (Hunt), and through loss of taste in the anterior two-thirds of the tongue in case of involvement of the chorda tympani.

While the cutaneous sensory area of the *N. facialis* in mammals persists thus as a mere vestige, the sensory trigeminal has gained importance. The main cutaneous supply of the face is through the *N. trigeminus*, which in mammals has evolved far above the ancestral reptilian plan. The cutaneous trigeminal field of mammals thus shows a high development similar to the motor facialis field. This may become evident from the discussion in the following two chapters.

V. THE EVOLUTION OF THE CUTANEOUS FIELD
OF THE N. TRIGEMINUS IN THE MONOTREMES,
CULMINATING IN THE ACQUISITION
OF HIGH SENSITIVITY OF THE SNOOT

In the *Monotremes* the evolution of the cutaneous trigeminus field culminates in the rich sensory supply of the snout region, which is covered with a thin horny cuticle in *Echidna*, and with a smooth, soft (not leathery (!), Burrell, 1927, p. 10) flexible skin in *Ornithorhynchus*, bare of tactile vibrissae in both forms (fig. 20). A series of authors have searched in vain for traces of such vibrissae. This complete absence of tactile vibrissae in the monotremes, in contrast to the marsupials and placentals, has been explained through deterioration of such structures in connection with the modification of the snout (Maurer, Pocock and others).

The absence of vestiges of vibrissae-movers such as the *M. maxillo-naso-labialis* and *M. mentalis* in the monotreme ground plan of superficial facialis musculature would rather suggest that the monotremes never possessed actively movable tactile

vibrissae on the snout (Huber). Other facts,—above all the peculiar, distinct arrangement of the sensory nerves to the snout (Huber)—support this conclusion. The acquisition of high sensitivity over the whole snout evidently offered a similarly efficient or, in the case of *Ornithorhynchus*, an even more efficient mechanism than a snout beset with tactile vibrissae.

Ornithorhynchus is most instructive because in this animal the tactile sense of the snout ("oral sense") exceeds by far the olfactory sense (compare Elliot Smith, 1899), although the olfactory apparatus is by no means deteriorated. Jacobson's organ, part of this mechanism, is, indeed, very well developed in *Ornithorhynchus* (Symington, 1891; Elliot Smith, '95; Hines, 1929). Profound modifications of the snout including its skeleton have taken place in *Ornithorhynchus*. While in *Echidna* the prenasal processes of the intermaxillary bones jointly with the nasal bones form the roof of the nose (fig. 22c) in *Ornithorhynchus* (figs. 22a and c) these processes no longer meet in the middle line. The large nasal bones have expanded further rostralward, splitting the intermaxillary bones widely apart. The anterior end of the upper jaw is thus considerably broadened, and the large interspace between the intermaxillary bones is filled out with a cartilaginous plate. Over this queerly modified flattened end of the upper jaw the smooth, delicate, flexible skin is stretched, and the snout is thus transformed into a structure which indeed closely resembles a duck bill in shape (fig. 20). The end of the lower jaw is adjusted to this bill.

From not less than fourteen distinct foramina on the upper and lower surface of both upper and lower jaw (figs. 22a—d), large cutaneous branches of the trigeminal nerve emerge to supply the bill (figs. 21c).

These nerve branches have been carefully traced by the author to their exit from the foramina. This was all the more desirable as some of those foramina have been misinterpreted by paleontologists (O. Abel, 1922, p. 387, 391/392, and figs. 1 and 5; see also M. Weber, 1927/28, vol. II, p. 33/34, fig. 7) as vestigial alveoli for incisor and canine teeth. After exclusion of these teeth, the vestigial temporary molar teeth in the upper and lower jaw of *Ornithorhynchus* can now definitely be considered to be the last and only remnants of the monotreme dentition (Huber).

The rich supply of the snout with cutaneous branches of the *N. trigeminus* accounts for the enormous size of the sensory portion of this nerve (figs. 21a and b; see further Koelliker, 1901, p. 97; Elliot Smith, 1899, p. 320/321, 323/324, and fig. 1; Hines, 1929, fig. 46b) and the remarkable dimensions of the corresponding nucleus (see fig. 21b, *tuberculum quinti*, compare further Koelliker, 1901, p. 97).

The cutaneous trigeminal branches end in Pacinian-like tactile corpuscles located in groups of two to three at the base of peculiar epithelial structures, the "push-rods", which are in large numbers scattered over the entire muzzle (E. B. Poulton, '94; Wilson and Martin, '94). Through so rich a supply of special sense organs the duck-bill-shaped snout of *Ornithorhynchus* is turned into an extraordinarily sensitive organ fit for searching the weeds and mud of the Australian rivers for eggs and larvae of aquatic fauna, worms, small crustaceans (shrimps) and little bivalves, as has been described by a series of authors (compare e. g., Burrell, '27).

Also in *Echidna*, just as in *Ornithorhynchus*, the sense of smell together with tactile sense of the snout are the directing senses, while sight and hearing evidently play a minor rôle. But in *Echidna* in contrast to *Ornithorhynchus* the "oral sense" stays far behind the enormously developed olfactory sense (compare Elliot Smith, 1899). The cutaneous branches of the *N. trigeminus* are therefore of correspondingly smaller

dimensions (fig. 22f), and the foramina in the skull and lower jaw (fig. 22e) are of accordingly moderate size. The arrangement of these foramina is, however, the same as in *Ornithorhynchus*, and fundamentally different from the marsupio-placentalian plan (Huber).

Tactile sense of the snout ("oral sense") added to the olfactory sense, with which it is closely linked, must have given the monotremes a considerable advantage over their reptilian ancestors, which probably used the tongue as tactile organ, just as

many modern reptiles do. The evolving "oral sense", demanding its representation in higher cortical centers immediately adjacent to the rhinencephalon, was probably one of the important factors in the evolution of the monotreme neopallium.

Kappers was the first to refer to a probably existing correlation between "oral sense" and neopallium development (Kappers, 1908, p. 523; Kappers and Theunissen, 1908, p. 279/280; see further Edinger, 1911, vol. I, p. 383/384; Kappers, 1920/21, vol. I, p. 333, vol. II, p. 911, 1202).

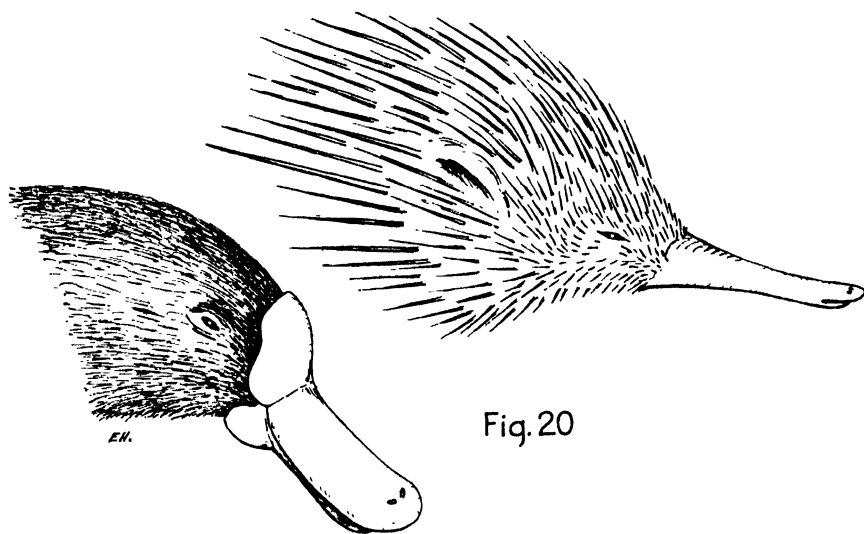


Fig. 20

FIG. 20. ECHIDNA, THE SPINY ANT-EATER WITH THE ELONGATED SNOOT COVERED WITH A SMOOTH, THIN, HORNY CUTICLE, AND ORNITHORHYNCHUS, WITH THE DUCK-BILL SHAPED SNOOT COVERED WITH A SMOOTH, SOFT, FLEXIBLE SKIN

At the base of the beak in the latter there are two shield-shaped, naked skin flaps, which protect the fur covered face above and below. Notice that in both monotremes there are no facial vibrissae, either on the modified snout or in the rest of the face. In *Ornithorhynchus* the orifice of the auditory meatus situated right behind the eye (compare fig. 5) is hidden in the thick fur. In *Echidna*, on the other hand, the anterior upper edge of the spoon-shaped ear cartilage (compare fig. 5) is seen as a slightly elevated structure over the surrounding skin, but there is no real external ear as in the case of the marsupials and placentals.

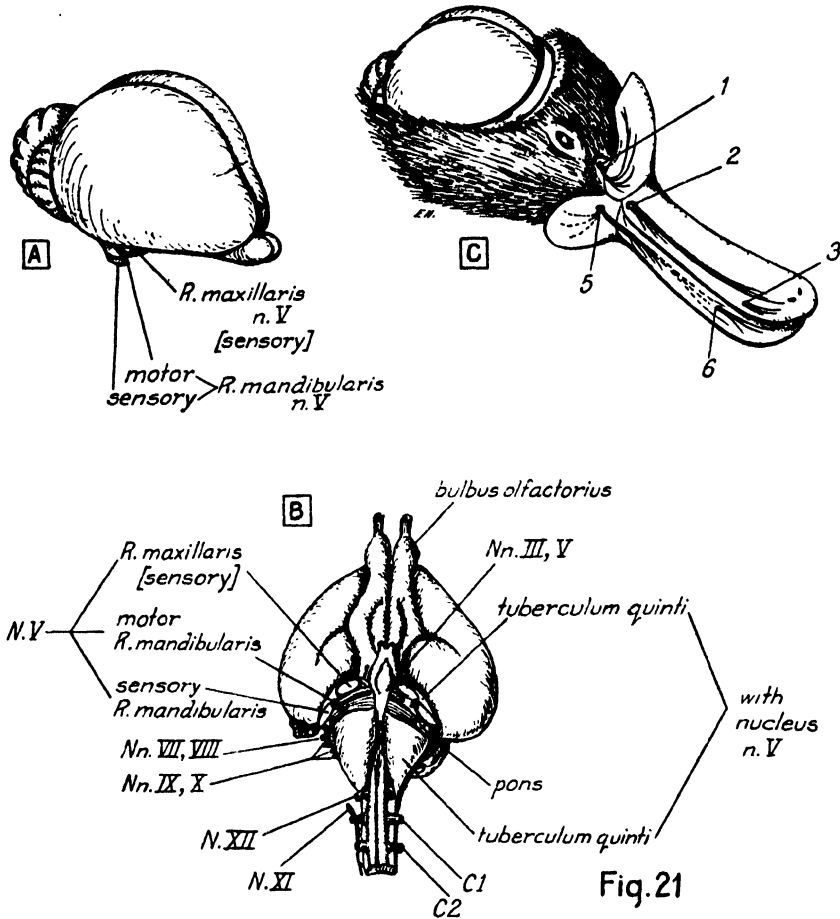


FIG. 21. THE BRAIN OF ORNITHORHYNCHUS WITH THE ENORMOUS N. TRIGEMINUS (A & B), AND THE CUTANEOUS BRANCHES OF THIS NERVE TO THE DUCK-BILL SHAPED SNOUT AND ITS SHIELD-LIKE PROJECTIONS (C)

a (by combination). At the base of the practically unfurrowed brain the large sensory *ramus maxillaris* and the large sensory portion of the *ramus mandibularis* joined by the small motor portion of the *N. trigemini* are indicated by stumps. Notice the comparatively large olfactory bulbs (compare also fig. 21b). Although in *Ornithorhynchus* the olfactory brain is by no means as highly evolved as in *Echidna*, the sense of smell (by the way of the outer narial passages, as well as through the well developed Jacobson's organ, which opens into the oral cavity) probably plays an important rôle in the life of this animal.

b. Brain of *Ornithorhynchus* seen from below (slightly modified after Hines), showing the enormous size of the sensory portions of the *N. trigemini* contrasted with the other cranial nerves as well as with the first and second spinal nerves. The enormous "*tuberculum quinti*" contains the correspondingly well developed *nucleus n. trigemini*. The sensory part of the *N. trigemini* of *Ornithorhynchus* is, indeed, known to be larger than that of any other mammal.

c. (From a specimen of the National Museum collection, dissected by the author.) Large cutaneous branches of the *ramus maxillaris* and *ramus mandibularis n. trigemini* emerge from the skull to supply the bill and its shield-like projections. The rich sensory supply to the muzzle of *Ornithorhynchus* indicates that this is an exceedingly sensitive organ, ideally adapted for searching the mud and water plants of the Australian rivers for aquatic fauna, which constitute the food of *Ornithorhynchus*. According to Burrell (1928) *Ornithorhynchus* keeps eyes and ears tightly shut under water, feeling its way with the aid of the highly evolved "oral sense." *Echidna*, on the other hand, is largely guided by the sense of smell, although tactile sense of the snout, especially of the tip of the snout, plays an important rôle (compare legend to fig. 22).

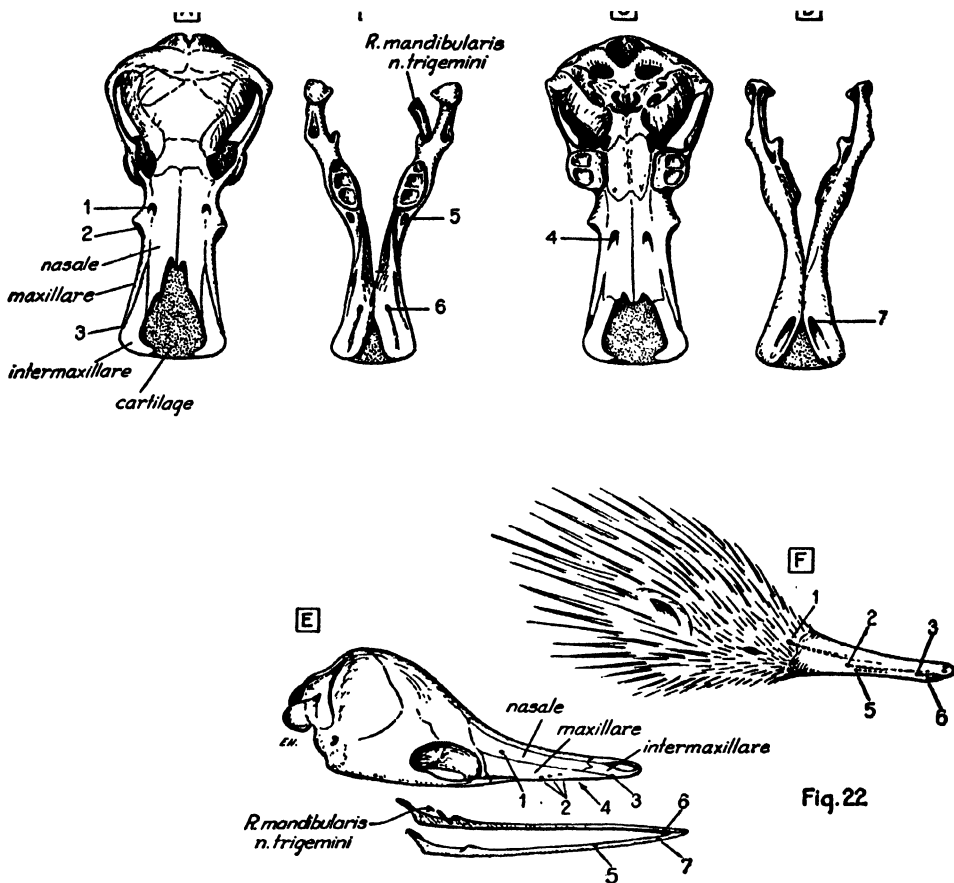


Fig. 22

FIG. 22. SKULL AND LOWER JAW OF ORNITHORHYNCHUS AND ECHIDNA (FROM SPECIMENS OF THE COLLECTION OF THE NATIONAL MUSEUM, WASHINGTON), AND SENSORY SUPPLY TO THE SNOUT IN ECHIDNA

a-d. Ornithorhynchus. On the dorso-ventrally flattened upper jaw the intermaxillary bones are split wide apart, and the interspace is filled out with a cartilaginous plate (stippled). Similar modifications have taken place on the lower jaw. It should be emphasized that the cartilage indicated in the figures is only part of the cartilaginous plates of the jaws. A broad rim of cartilage outside and in front of the bony structures of the jaws considerably increases the width of these plates, which makes the bill very broad (compare e. g., Schimkewitsch, *Lehrbuch der vergleichenden Anatomie der Wirbeltiere*, 1910, fig. 146). On the upper and lower surfaces of both upper and lower jaw (fig. 22a-d) are shown the foramina (1-7) through which large cutaneous branches of the *N. trigeminus* emerge to supply the duck-bill shaped snout, as seen in the previous figure. The arrangement of these foramina is distinctly different from that of the marsupials and placentals; it is peculiar to the monotremes. Notice in figures 22b and c on the oral surface of upper and lower jaw the horny plates, which replace the vestigial, temporary molar teeth. These horny plates serve for crushing the shells of little bivalves which form an important part of the food of *Ornithorhynchus*.

e. Echidna, showing the same ground plan of trigeminal foramina on the skull and lower jaw as in *Ornithorhynchus*. There is a bilaterally placed foramen (1) on the upper surface of the nasal bone close to the nasomaxillary suture; three to four small bilateral foramina (2) laterally placed on the maxillary bone, evidently corresponding to the one large lateral foramen of *Ornithorhynchus*; one more, very small bilateral foramen (3) close to the tip of the elongated upper jaw in an exactly corresponding location as in *Ornithorhynchus*, at the junction of the maxillary bone with the intermaxillary bone; and one bilateral small foramen (4) on the lower (oral) surface of the maxilla in the same location as in *Ornithorhynchus*. Several little bilateral foramina are placed on the extremely slender mandible in the same locations as in *Ornithorhynchus*, one (5) considerably larger than the others, further back on the upper (oral) surface of the mandible, and two very small foramina close to the tip of the mandible on the inner (6) and outer surface (7) of this bone. Thus *Echidna* gets a considerable, though by no means as rich a supply of cutaneous trigeminal branches to the snout as *Ornithorhynchus*. The sensory part of the *N. trigeminus* in *Echidna* does not therefore reach such enormous dimensions as in *Ornithorhynchus*. Nevertheless the tactile sense of the snout plays an important rôle in *Echidna* as observed in the live animal. Notice in figure 22c that maxillary, intermaxillary and nasal bones form a rigid framework which encloses the nasal cartilage, in a similar way as in the reptilian plan. Because of the solid fusion of the individual bones in the skull of the adult *Echidna* the sutures are barely indicated in these places. The two mandibular bones however remain separate.

VI. ACQUISITION AND ELABORATION OF ACTIVELY MOVABLE TACTILE FACIAL VIBRISSAE IN THE MARSUPIALS AND PLACENTALS AN ESSENTIAL FACTOR IN THE EVOLUTION OF THE CUTANEOUS FIELD OF THE N. TRIGEMINUS, OF THE SUPERFICIAL FACIALIS MUSCULATURE, AND OF THE NEOPALLIUM

Characteristic of the ground plan of the *Marsupials* and *Placentals* are: a hair-free, moist and extremely sensitive mucous membrane patch at the tip of the snout (rhinarium), mystacial vibrissae implanted into a bilaterally placed tough connective tissue cushion on the upper lip, and a set of additional facial vibrissae on the chin, in the interramal region, in the supraciliary region and on the cheek in the field situated between the ear, the eye and the mouth cleft (fig. 23). These facial vibrissae are peculiarly specialized tactile hairs with their shafts developed into long bristles which project quite a distance from the head. The dermal sheath of each of these tactile hairs contains, between the lamina externa and interna, lacunar spaces filled with blood (fig. 24d). On account of these blood sinuses the tactile vibrissae have been termed "sinus hairs". Formation of such cavernous sinuses naturally increases the efficiency of these hairs as tactile organs. The slightest touch exerted upon the end of the long bristles transmitted through the stiff shaft to the springy cavernous hair sheath is thus extended over a larger sensitive area, and tactile impulses become intensified through this. The vibration of the loosely implanted hair shaft moreover prolongs the initial touch stimulus. Subliminal stimuli may through this be summated. Vibration of the hair shaft within the cavernous sheath of the follicle is undoubtedly of great importance. Many mammals, particularly small rodents, keep their heavily set, long mystacial vibrissae

in continuous titillating motion. It can be assumed that the slightest change in intensity of this vibration, resulting from even minute touch upon the quivering vibrissae, may be appreciated by the animal. The tactile stimuli are received by the sensory nerve endings of the hair follicles and their immediate surroundings. Sensory nerve fibres pierce in great number the dermal sheath of the follicles (compare fig. 24c) to form a heavy plexus over the outer root sheath. Fibres of this plexus terminate in the numerous touch cells which form a mantle in the outer root sheath all over the follicle (Bonnet, 1878; Vincent, 1913).

An elongated snout beset with tactile vibrissae, and a full set of additional vibrissae in the cited areas must have been striking features in the ground plan of the common ancestor of the marsupials and placentals. The development of tactile sense of the muzzle ("oral sense") improved through the large mystacial vibrissae, goes side by side with the perfection of the olfactory sense. The tactile vibrissae in the other regions of the face are important additions. That the facial vibrissae are of vital importance as tactile organs, becomes evident through plain observations on the behavior of marsupials and placentals. This has also experimentally been demonstrated. Even when blinded through destruction of the visual area in the occipital lobe, opossums were able to move about and avoid obstacles by the use of the delicate touch pressure of the facial vibrissae (Rogers, 1924).

Most instructive are Vincent's experiments performed in connection with investigations on learning in the white rat (1912). This comprehensive behavior study gives clear evidence that the facial tactile vibrissae, particularly the mystacial vibrissae, are powerful organs of touch, which aid the animal in locomotion and

equilibration, in determining nearness or position of edges or corners, and in determining inequalities of surface. They supplement the poor vision of the rat.

The facial vibrissae, in contrast to the ordinary, only slightly sensitive hairs, are brought under voluntary control, through portions of the superficial facialis musculature, which have become attached to the connective tissue patches where the vibrissae are implanted (compare figs. 7, 9, 11 and 24). These muscles are the *M. maxillo-naso-labialis* and *M. naso-labialis* for the mystacial vibrissae, the *M. mentalis* for the mental vibrissae, the *M. depressor supercillii* for the supra-orbital vibrissae, and portions of the platysma and *sphincter colli profundus* for the genal vibrissae (Huber). With the aid of this muscle apparatus the animals can move the vibrissae in different directions in order to bring them more freely in touch with the obstacles which are encountered along the trail. In the marsupials and in those placentals where the vibrissae are fully developed, vibrissae movements are an outstanding phenomenon in stimulation experiments on the facial area of the motor cortex. From a study of the findings of former authors one becomes aware that vibrissae movements were often believed to be a phenomenon occurring independently of the contraction of the facialis musculature. By exposing the superficial facialis musculature in opossum, cat and dog during the stimulation experiments it could be definitely proven that the vibrissae movements are indeed effected through contraction of the above mentioned muscles (Huber and Smith).

It is illuminating to view the different orders and suborders of marsupials and placentals in regard to the occurrence, distribution and manifold modifications of the facial tactile vibrissae. Scattered references to the distribution of the facial

vibrissae are found in the older and newer zoological literature. Noteworthy are the publications on this subject by Bonnet (1878), Haacke ('90), Maurer ('95), Frédéric (1905), Friedenthal ('08, '11), Schwalbe ('11), Pocock ('14), Henneberg ('15), Müller ('19), Wood Jones ('23). Pocock investigated systematically the occurrence of facial vibrissae throughout the orders of mammals except the whales, which latter have however been investigated by Japha (1912), and by a series of other authors. The communication by Pocock may serve as a guide for further, more elaborate investigations on this field, which promises to be of great value also from the standpoint of systematic zoology. The author himself in his investigations on the facialis musculature has studied the distribution of the facial vibrissae. A brief sketch, whereby the findings of Pocock and others are utilized, may here summarize some fundamental data:

For most *Marsupials* a complete set of facial vibrissae is characteristic.

In the *polyprotodont marsupials* these vibrissae are generally found in a high state of development. A rare exception among this group is *Notoryctes typhlops*, a digging marsupial type adapted like *Talpa* among the placentalian insectivores. In *Notoryctes* the vibrissae are completely deteriorated on the elongated snout, which is covered with a rigid horn plate.

In the *diprotodont marsupials* (compare fig. 8) the facial vibrissae are usually shorter and less numerous than in the polyprotodont marsupials.

Among the *Placentals* in many *Insectivores*, *Bats*, most *Carnivores* (the bears exempt), in *Rodents* and in the *Prosimians* (compare next chapter on the Primates) the typical primitive distribution and development of facial vibrissae is found in full correspondence to that in the marsu-

pials. The other orders of the placentals show manifold modifications. Within the heterogeneous group of the "Edentates" the facial vibrissae are deteriorated in the anteaters (*Tamandua*, *Manis*, *Myrmecophaga*) and in the slow climbers (*Bradypus* and *Choloepus*), while in the armadillos they are retained, often hardly distinguishable from the ordinary hairs. Moderately long and fine facial vibrissae persist in many *Ungulates*, while they are aborted in other representatives of the ungulate stock, e. g., in the Rhinoceros and Hippopotamus. Scanty vibrissae vestiges are found on the proboscis of the *elephants*.

Most interesting are the modifications of the facial vibrissae in *mammals with aquatic adaptation*. Even some of the aquatic *fissipede carnivores* (e. g., the otters) show greatly enlarged mystacial vibrissae, while, on the other hand, the polar bear has the vibrissae reduced, just as the whole bear stock from which the polar bear sprang. The very broad, sensitive rhinarium characteristic of the bears, may here substitute for the mystacial vibrissae.

In the *Pinnipedes* the mystacial vibrissae are represented by long stiff bristles (compare fig. 24a), which are thicker than those of any other mammal. They have a characteristic arrangement in the different pinniped genera and species (Huber). A large bundle of nerve fibers from the *N. infraorbitalis* connects with the bulbs of these huge sinus hairs and with their immediate surroundings (fig. 24b). This makes the whiskers of the pinnipeds an effective mechanism for appreciation of slight changes in water pressure. The pinnipeds may thus avoid injuries to the guiding head and the following body while they swiftly swim about and boldly dive along rocky shore lines, or while they play tumultuously amidst irregularly shaped ice cakes in the far north.

In the group of *Sirenia*, slow marine

mammals, on the other hand, the vibrissae on the strangely modified upper lips, i. e., the mystacial vibrissae, are short tough bristles, which aid the animals in grazing on the bottom of the sea.

In the *Whales*, the most highly specialized marine mammals, we find the most remarkable modifications of the facial vibrissae apparatus. For the whale, acquisition of a highly sensitive mechanism for appreciation of changes in water pressure, an apparatus with the same function as the lateral-line organs in fishes, was a prerequisite for successful adaptation to exclusively pelagic life. In this, as in so many other points, the two groups of living whales, the tooth whales and the whale-bone whales, have differentiated along separate lines.

The *whale-bone whales* (Mysticeti) possess a large number (up to over 130, according to M. Weber) of peculiarly modified mystacial and mental vibrissae (compare also fig. 25c). While the bristles of these tactile hairs are vestigial their hair sheaths persist, and the blood sinuses therein have reached further extension and elaboration. According to Japha every one of these tactile hairs is supplied with several hundred myelinated nerve fibers, with which tactile Pacinian-like corpuscles are connected. The occurrence of Pacinian corpuscles in connection with hairs is peculiar to the whales.

In the *toothed whales* (Odontoceti) vestiges of similarly modified mystacial vibrissae are found only during fetal life (fig. 25a). The functionally important tactile vibrissae apparatus is replaced presumably, according to the author's interpretation, by other mechanisms, the "melon" in all the toothed whales with the exception of the physeterids, and its corresponding structure, the "junk", and possibly the spermaceti cushion, in the aberrant odontocete group of the physeter-

ides. The "melon" is a peculiar accumulation of modified fatty tissue just in front of the blowhole (figs. 25b). It is richly supplied with cutaneous branches from the huge infraorbital nerve (fig. 25c), which leave the skull through as many as 6-9 separate bilateral foramina (fig. 25d) far apart from each other (Huber). The multiple emergence of these sensory nerves is evidently secondary, for there is just one large foramen for the *N. infraorbitalis* in archaic fossil whales among the extinct group of the zeuglodonts, as noticed in various museum specimens.

The modified tactile vibrissae apparatus in the whalebone whales, the "junk" and the spermaceti cushion in the physeterids, and the "melon" in the rest of the toothed whales, have been interpreted by the author as hydrostatic organs. Both the toothed whales and the whalebone whales are dependent on such a mechanism. Without it they could not possibly have become successfully adapted to exclusively pelagic life. The delicate sensory apparatus on the snout of the whalebone whales would naturally also assist these strangely specialized mammals in their pursuit of plankton (Japha), which they take in enormous quantities. Most of the toothed whales, on the other hand, which feed on larger animals like fishes and large cephalopods, or Orca, the fierce "killer", which feeds on mammals (seals, porpoises and even bigger whales), are guided in their food pursuit by vision. One exception to this is the aberrant, blinded *Platanista*, which lives in muddy rivers, mainly feeding on crustaceans (M. Weber). It would be important to learn whether the numerous sinus hair anlagen which have been reported to exist on the upper and lower jaws in *Platanista* fetuses (Weber, 1927/28, vol. II, p. 355), possibly develop into modified tactile organs similar to those of the whalebone whales.

It is through the *N. trigeminus* that all the tactile facial vibrissae receive their sensory innervation. The cutaneous branches of this nerve are, indeed, most abundant in the areas where the facial vibrissae are implanted, and we have good reason to assume that the various vibrissae groups determined the locations where individual cutaneous trigeminal branches should emerge from the skull (Huber).

There exist, naturally, modifications according to the construction of the skull, as in regard to the formation of the zygomatic arch, the bony frame of the orbit, the shape of the maxilla, etc. Moreover, the foramina may be duplicated or multiple. This seems to be characteristic for certain groups of the placentals, so that the arrangement of the trigeminal foramina might become of some systematic value. The individual variability, however, is great.

The established plan of distribution of these foramina for the respective cutaneous branches of the *N. trigeminus* in the lower primates, presumably determined by the arrangement of the facial vibrissae groups (see chapter VII), is retained throughout the ascending scale of primates, despite the deterioration of the vibrissae as tactile structures. Thus we find in man (fig. 26) in the same locations the *foramen infraorbitale* for the *N. infraorbitalis*, the *foramen supraorbitale* or *incisura supraorbitalis* for the *rami supraorbitalis* and *frontalis* of the ophthalmic division of the trigeminal nerve, the *foramen zygomaticofaciale* for the *N. zygomaticofacialis*, and the *foramen mentale* for the *N. mentalis*. Multiplication of these foramina are not uncommon variations and have often been referred to in the anatomical literature.

The studies on the facial vibrissae and their innervation lead to the conclusion that the evolution of the sensory field of the *N. trigeminus* in marsupials and

placentals is closely linked with the acquisition of these facial tactile vibrissae (Huber). And there is clear evidence that the elaboration of this important head protecting and guiding mechanism of tactile vibrissae, actively movable through facial muscles, was one of the causal factors in the evolution of the marsupio-placentalian ground-plan of the superficial facialis musculature (about other causal factors, see Huber, *Morphol. Jahrb.*, 1922/23, p. 400).

Requiring sensory as well as motor representation in higher, cortical centers, the evolving facial tactile vibrissae apparatus of the common ancestors of the marsupials and placentals must thus also have played an influential rôle in the early stages of evolution of their neopalium (see also Kappers, 1908, 1920/21; Edinger, 1911; Wood Jones and Porteus, 1928, pp. 99, 167, and others).

(To be continued)

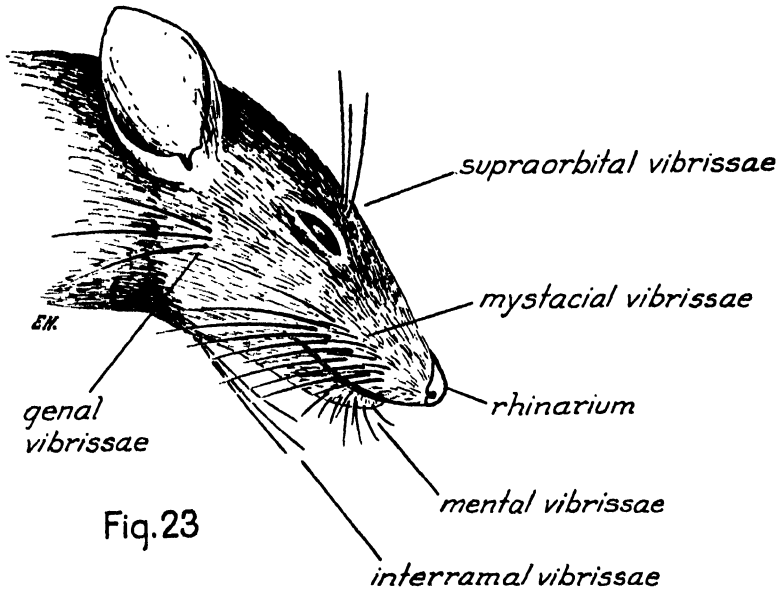


Fig. 23

FIG. 23. SCHEME OF THE ARRANGEMENT OF THE FACIAL TACTILE VIBRISSAE WHICH ARE CHARACTERISTIC OF THE MARSUPIO-PLACENTALIAN GROUND PLAN

The facial vibrissae are arranged in definite groups (supraorbital, mystacial, mental, interramal and gena¹ vibrissae). They receive their sensory supply from cutaneous branches of the *N. trigeminus*. Unlike the ordinary hairs these vibrissae (sinus hairs, compare further figs. 24c-e) are under voluntary control of facial muscles, which are inserted into the connective tissue patches into which the vibrissae are implanted, as shown in previous figures of chapter 1. (Compare figs. 7, 8, 9, 11.) Notice that in contrast to the monotremes, only the tip of the snout is naked in the marsupials and placentals. It forms the rhinarium, which is a moist, extremely sensitive mucous membrane patch. The rhinarium jointly with the mystacial and mental vibrissae serves the "oral sense" (tactile sense of the snout), which is closely associated with the olfactory sense. Yet the rhinarium is not only essential as a tactile structure, but owing to its moist and comparatively large sensitive surface it is of great assistance in quickly informing the animal about the direction of scent carried to the nose by the lightest wind. Also in this function it supplements the olfactory mechanism. The mystacial vibrissae and the rest of the facial vibrissae on the other hand form a vitally important protective mechanism. It is not astonishing that this should be best developed on the head, the guiding part of the body. Additional tactile structures, the carpal and tarsal vibrissae, likewise sinus hairs, and the guarding hairs of the fur serve as guiding mechanisms and belong to the marsupio-placentalian ground plan. While this primitive ground plan has been retained in a host of marsupials and in many primitive placentals, it has in other representatives of the placentals become modified and specialized along many lines.

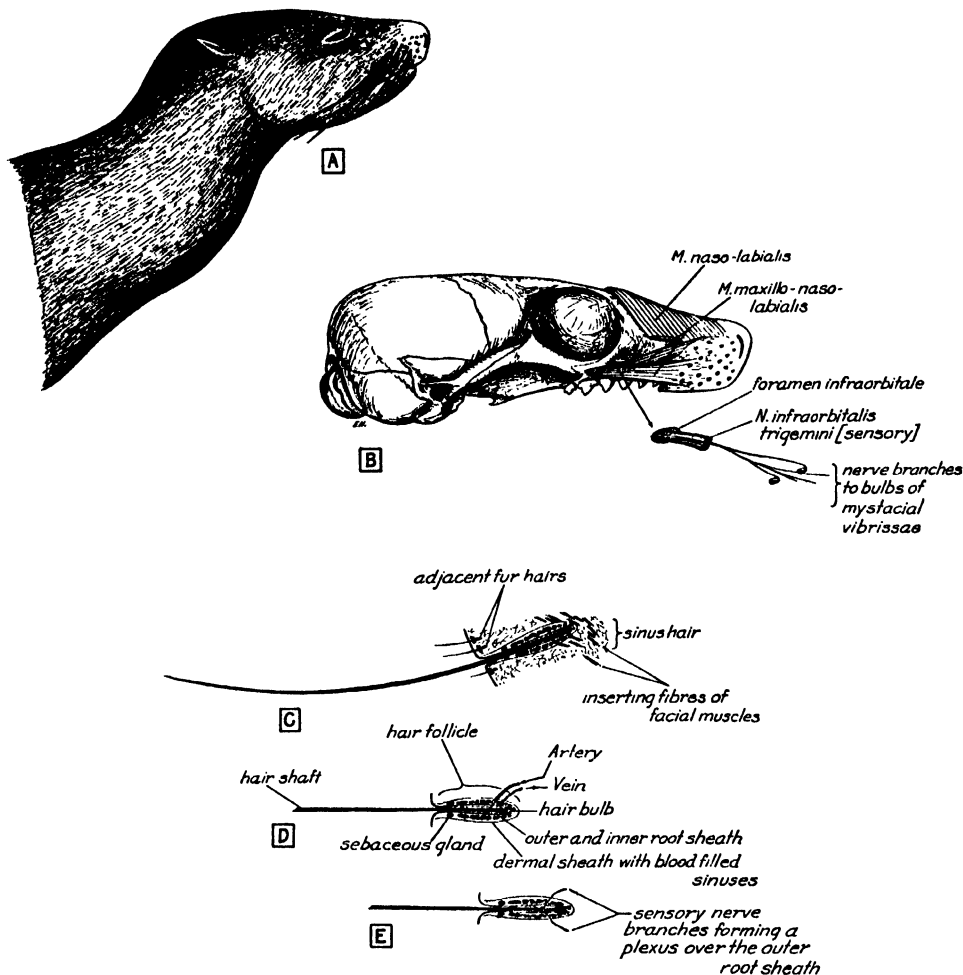


Fig.24

FIG. 24 A AND B. SEA-LION (*ZALOPHUS CALIFORNIANUS*) OF THE JOHNS HOPKINS COLLECTION, SHOWING THE LONG, STIFF MYSTACIAL BRISTLES

Of all the mammals the sea-lions and seals possess the largest mystacial vibrissae. *b* shows the skull of a sea-lion with the soft parts of the snout. Bilaterally placed there is a tough connective tissue cushion into which the mystacial bristles (cut) are implanted. Facial muscles, the *M. maxillo-naso-labialis* and *M. naso-labialis*, insert into this cushion, and bundles of these muscles connect with the bulbs of the sinus hairs, which are thus put under voluntary muscular control. From the large infraorbital foramen emerges the unusually thick *N. infraorbitalis trigemini*. In the additional little figure a branch of this sensory nerve is shown with twigs terminating on the bulbs of the mystacial bristles and in their immediate surroundings. The highly sensitive mystacial vibrissae are of vital importance for the pinnipeds, as already emphasized in the text.

c-e. A schematic representation of the topography and structure of the sinus hair.

c, showing a sagittal section through the skin, with a sinus hair in situ, and 3 small adjacent fur hairs. The large shaft of the sinus hair projects a long distance above the surface of the skin, while the large follicle of the sinus hair is lodged deep in the subcutaneous tissue. A few striated muscle fibres of the facial musculature are seen inserting into the follicle.

d, showing a large artery entering the dermal sheath of the sinus hair. It leads into the elaborate blood sinuses of the follicle, while the accompanying vein drains these sinuses. The cavernous, blood-filled dermal sheath of the follicle thus forms a springy cushion, into which the root of the hair shaft, invested with the outer and inner root sheath, is implanted. At the neck of the hair follicle sebaceous glands drain into the follicle cavity. The secretion of these sebaceous glands oils the hair shaft and thus keeps the bristle elastic.

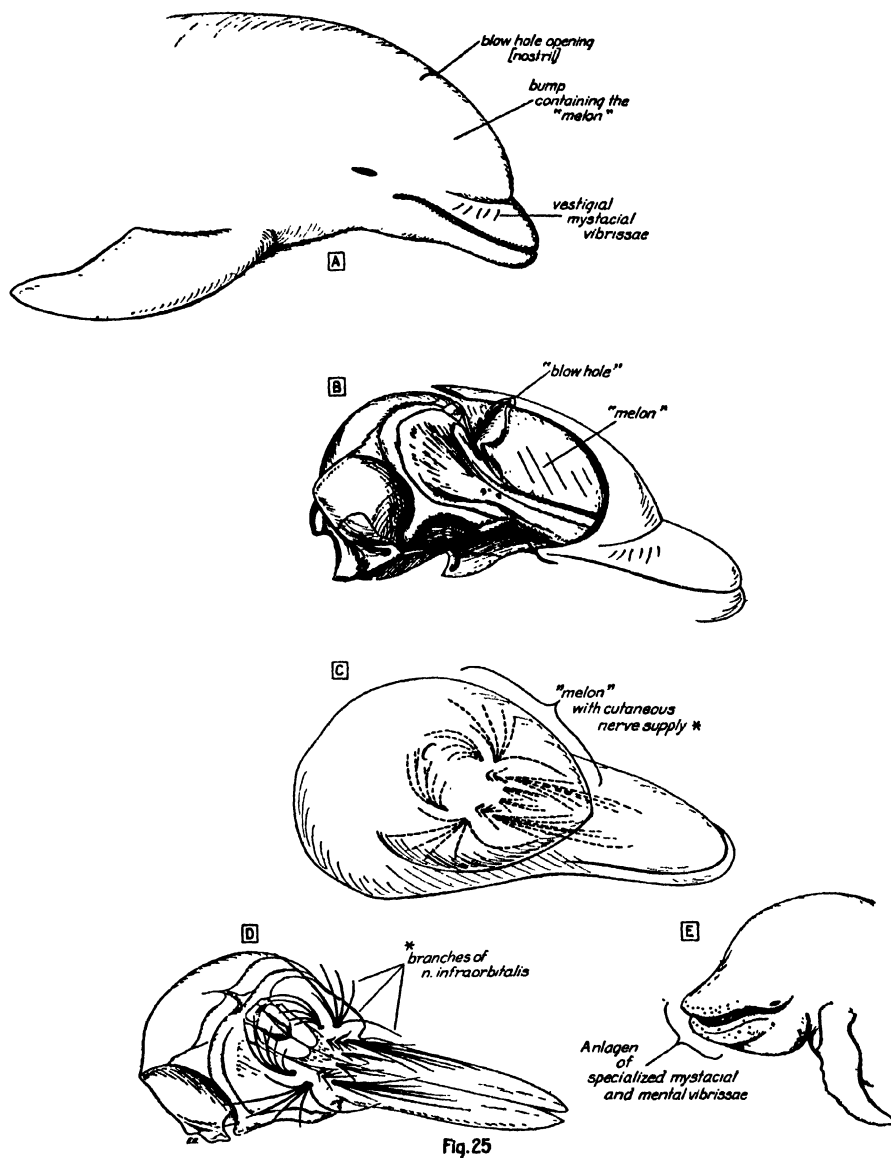
e, showing the sensory nerve supply to the sinus hair. Two cutaneous branches of the trigeminal nerve, composed of a large number of fibres, are seen entering the hair follicle. After having pierced the dermal sheath the nerve fibres spread out to form a dense plexus over the outer root sheath. Terminal fibres from this plexus connect with the "tactile cells of Merkel" lodged in the outer root sheath.

FIG. 25 A-D. ALMOST FULL TERM FETUS OF A PORPOISE (*Tursiops truncatus*) REPRESENTING THE TOOTHED WHALES (COLLECTION OF THE NATIONAL MUSEUM, WASHINGTON), AND (E) EARLY FETUS OF A WHALEBONE WHALE (JOHNS HOPKINS COLLECTION)

a. Notice the vestigial facial vibrissae on the upper jaw of the porpoise. Vestigial vibrissae, which generally occur in this location in fetuses of toothed whales, indicate that the ancestors of the Odontoceti must have had mystacial vibrissae in an arrangement similar to that of the sea-lions (fig. 24) and seals. These vibrissae, doubtless of high functional importance in the early ancestors of the whales, were the last hairy structures to disappear together with the other structures which might cause friction in fast swimming. The function of the mystacial vibrissae as tactile, and possibly hydrostatic, organs must have been taken over by new structures, presumably by the "melon" in most of the toothed whales, or by the "junk" and the spermaceti cushion in the aberrant odontocete group of the Physeteridae.

b. The "melon" is a peculiar accumulation of a special fat with low solidification point. The "melon" rests upon the upper jaw just in front of the blow-hole. It is richly supplied with cutaneous branches of the *N. infraorbitalis trigemini* (fig. c) which emerge through 6 to 9 distinct bilateral foramina from the upper surface of the maxilla (fig. d). The "junk" and the spermaceti organ of the Physeteridae are similarly placed on the head and contain a specialized fat different in composition from the ordinary fat of the subcutaneous tissue.

The whalebone whales, on the other hand, possess numerous, shaftless sinus hairs on the upper jaw and chin. Notice in figure 25e the anlagen of these structures in an early fetus of a whalebone whale. These peculiarly modified mystacial and mental vibrissae have very elaborate blood sinuses and receive an extraordinarily rich supply of myelinated nerve fibres with which tactile Pacinian-like corpuscles are connected. Various investigators who have had a chance to examine live, stranded whalebone whales found in these animals the areas of the sinus hairs extremely sensitive. It is indeed conceivable that such an elaborate, highly sensitive tactile mechanism may also function as a hydrostatic organ. A guiding hydrostatic organ seems indispensable for fast swimming and deep diving marine animals. Without acquisition of an effective hydrostatic mechanism of some kind the whales could not possibly have become ideally adapted to exclusively pelagic life.



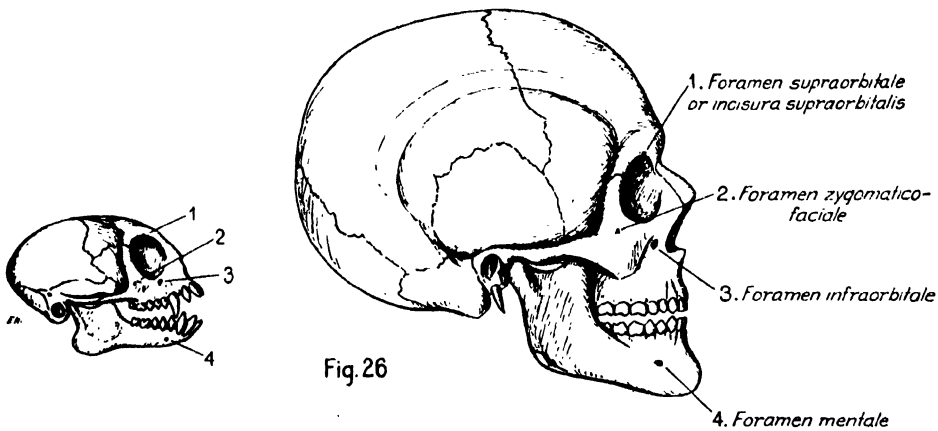


FIG. 26. SKULL OF A PRIMITIVE PRIMATE (*CALLITHRIX*) AND OF MAN TO SHOW THE ARRANGEMENT OF THE TRIGEMINAL FORAMINA

The locations of these foramina in the lower primates appear to be determined by the groups of facial tactile vibrissae, which receive their innervation through the corresponding cutaneous branches of the *N. trigeminus*. Examination of a large series of skulls of representatives of the various groups of the primates (collection of A. H. Schultz, Baltimore) revealed the fact that the established ground-plan of these foramina is retained throughout the "ascending scale of primates" up to man, despite the deterioration of the facial vibrissae as tactile structures in the higher primates. The variability in size and arrangement of the trigeminal foramina is considerable, and increase in their number is of common occurrence. In certain genera this multiplicity of foramina appears to be the rule rather than the exception. Thus in higher platyrrhines, and in the lower catarrhines the *foramen infraorbitale* may be replaced by 3, 4, 5 small foramina usually grouped in a cluster in the place where we should expect a single foramen. However, these small foramina may be arranged in a row along the infra-orbital margin as in certain representatives of the baboons. In others, especially in long snouted baboons, the group of smaller infraorbital foramina came to be scattered over the upper surface of the maxilla, evidently because of the extreme growth of the maxilla. In the gibbons and in the great anthropoid apes the infraorbital foramina tend to be reduced to a single foramen. In man this seems to be the rule, although double foramina are not unusual.



DIURNAL MIGRATION OF PLANKTON CRUSTACEA

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EVER since Forel and Weismann studied the daily vertical movements of the various plankton crustaceans in lac Léman and the Bodensee in 1874, various observations and experiments have been carried out to account for such migrations. The results show that diurnal migration is a very complex phenomenon, that there are great variations in the movements of different species and that the types of migrations shown by each species are quite similar from day to day in each lake. In a few cases, it has been noted that not only is the type of movement of a single species not the same in all lakes, but the character of the migration of a species sometimes changes in the same lake. Experiments indicate that the causes of the migration are not necessarily the same in all cases and it is therefore impossible to apply the facts learned from one species to others. Furthermore the simultaneous vertical movements of different species may sometimes result from quite different causes.

Before Groom and Loeb (1890) explained plankton migrations on the theory of phototropism, various interpretations had been given. Forel (1874) supposed that plankton sank during the day because the wind blew toward the land, and would drive the plankton ashore if it remained near the surface, while in the night plankton came nearer the surface because the wind blew from the shore. Weismann (1877) was of opinion that the crustaceans performed daily vertical movements because their eyes were adapted to a

low intensity of light, and were thus suited for getting food at night. A similar explanation was accepted by Fuchs (1882). Chun (1887), however, opposed this view and came to the conclusion that the diurnal migration is due not so much to the effect of light as to the influence of temperature. The later observations showed the importance of the interrelations of light and gravity as factors affecting the diurnal vertical movements. It was shown that temperature may secondarily affect vertical distribution of plankton.

In this paper the writer discusses the observations and experiments relating to vertical migrations of plankton organisms and attempts to give an account of the present status of scientific knowledge relating to such phenomena.

THE EXPERIMENTAL STUDY OF DIURNAL MIGRATIONS

The first paper bearing on the diurnal migration of plankton from the experimental side was published by Groom and Loeb (1890). These investigators worked with the nauplii of *Balanus* and reached the conclusion that these animals move down by day because they are negatively phototropic to strong light and come nearer the surface towards night because they are positively phototropic to faint light. Loeb (1893) later found that *Daphnia*, *Polygordius* larvae, and *Temora longicornis* became positively phototropic when the water surrounding them was cool, but were negatively phototropic in warm

water. By adding sodium chloride to sea water, the same species of animals were shown to become positively phototropic and a decrease of salinity had the same influence as the warming of the water. Loeb further found (1904, 1906) that copepods, *Daphnia*, the nauplii of *Balanus*, and *Gammarus* were made positively phototropic by adding carbon dioxide or other acids. A general conclusion based on these experiments was given by Loeb in 1908. He states that as the temperature of surface water falls and CO₂ content increases toward night, positive phototropism is induced in animals, while in the morning, when the surface water is warmed by the sunlight and the CO₂ content decreases because of the photosynthetic activity of phytoplankton, animals become negatively phototropic. All these factors were affirmed to cause an animal to move down from the surface by day and come nearer the surface at night. In the daytime animals are believed to descend until they reach cold water, where they become positively phototropic. Loeb regarded gravity and the viscosity of water as additional factors influencing migration. He (1914) later added "the periodic changes in the internal chemical processes of the organism in relation to the phototropism" as another accessory factor. However, it is quite improbable that the actual daily changes in the temperature and carbon dioxide content of the water of a lake or of the open ocean are large enough to change phototropism from positive to negative or vice versa.

Bauer (1908) found that *Macropsis*, a mysid, showed a tendency to positive phototropism in horizontal rays, while it swam downward in the same intensity of light from above. This fact does not agree with Loeb's theory. Perhaps such behavior is due to a strong positive geo-

tropism induced by light, as Dice (1914) has suggested.

Parker (1901) states that the females of the copepod, *Labidocera aestiva*, swim down in the morning because they are negatively phototropic to strong intensities of light and move up in the evening because they are positively phototropic and negatively geotropic in weak light. He states that the females show more strongly marked negative geotropism than the males. The females are positively geotropic in water warmer than 26°C, though negatively geotropic in colder water. Parker further suggests that the males follow the females in their migrations because they are probably positively chemotropic to them.

The reversal of geotropism with the change of the intensity of light was first observed by Esterly (1907) in the female of *Cyclops albidus*. He found that the female of *Cyclops* is ordinarily positively geotropic, but after having been in light such animals tend to become negatively geotropic in darkness. He further states (1912) that sooner or later such an animal becomes again positively geotropic in the dark without any change in external conditions. He offers a possible explanation of diurnal migration based on the effect of light upon geotropism. The same phenomenon was observed by Harper (1907) in *Corethra* larvae, by McGinnis (1911) in *Branchippus serratus*, and by Dice (1914) in *Daphnia pulex*.

Dice (1914) studied the reactions of *Daphnia pulex* to various factors, such as light, gravity, temperature, chemicals, mechanical stimuli, locomotor activity of the organism, and age of individual with particular reference to vertical movements. He shows that an increase in temperature has a tendency to decrease the positive phototropism, while a decrease tends to make the animals more strongly positive.

At temperatures below 12°C. they are positive to all intensities of light. Increase of light intensity and high temperature cause a tendency to positive geotropism, while decrease in light intensity and low temperatures produce a tendency to negative geotropism. Dice came to the conclusion that the reversal of geotropism with the change of light intensity is a predominant cause in affecting the diurnal vertical movements of *Daphnia pulex*. He regarded phototropism as an accessory factor which determines the upper and lower limits of vertical distribution.

THE WORK OF ESTERLY

An important paper by Esterly (1919) deals with experiments on the phototropism and the geotropism of marine copepods and chaetognaths, with special reference to the diurnal migration. Two very important characters of *Acartia* were pointed out. First, Esterly showed that specimens obtained from the surface water react in different ways to light, gravity, and temperature than those obtained from deep water. The latter, however, react in all respects as do the animals from the surface water after they have been kept in a laboratory for a time. In the second place, he pointed out that there is a physiological rhythm in connection with the geotropism of species. This does not appear to be connected directly with external changes occurring at the time. Esterly observed that the animals are found largely toward the bottom of a glass tube when kept in the dark during the day. But from 6 p.m. to 8 p.m. there is a noteworthy increase of animals at the top, even if surrounding conditions are kept the same as before.

Esterly reached the general conclusion that each species has its own way of performing vertical movements and no general explanation of the diurnal migra-

tion can be given at present. It appears that changes in geotropism with changes in light intensity or in temperature are not general enough to be considered as of wide significance. The possible bearings of the experiments on the diurnal migration of each species are given in connection with the field observations made by Esterly in the San Diego Region, 1905 to 1911. The absence of the plankton copepods from the surface of the sea during the day may be explained by the fact that they are negatively phototropic to strong light. Esterly is quite positive that in *Acartia* the physiological rhythm of the animals ought to be considered as the primary cause affecting the upward movement in the evening. There is some evidence of a similar condition in *Calanus*. The field data show that these copepods leave the surface in the early part of the night. Positive geotropism in darkness may explain the downward movement in the dark and there will be no need to relate the movements to a response to light. When the physiological state that prevails during the time that the animals show negative geotropism is changed, the downward movement will begin. The movement of *Labidocera* might be explained in a similar way. In the case of *Sagitta*, light intensity is apparently the determining factor for diurnal migration. It is to be expected that this animal will leave the surface of the sea as the light grows brighter, because it shows strong positive geotropism in bright light. It also seems clear that in the more subdued light it will begin to ascend, because it shows positive phototropism and negative geotropism in such low intensities of light. It is not clear why *Eucalanus* and *Metridia* come up near the surface in spite of the fact that they show positive geotropism in warm water in darkness.

Rose (1925) examined the reactions of

various marine planktons to light, temperature, salinity, and chemicals. He found that *Phialidium*, *Pleurobranchia*, and *Sagitta* show no phototropism in any intensity of light, but react in a different way when there is a change in temperature and salinity. All the Crustacea of the plankton studied show a marked phototropism which is influenced by changes in temperature, acidity, and chemicals. Rose states that the diurnal migration of plankton is due to the influences of external factors. The change of phototropism with changes of light intensity and temperature is believed to be the chief cause. The effect of temperature becomes very important when it passes 20°C. As additional factors in relation to the phototropism of organisms are given salinity, chemical content of the sea water, and dissolved gases. The internal physiological condition of the animals may also be regarded as a factor.

Fox (1925) carried out experiments concerning the effects of light on the vertical movement of *Paramecium* and echinoid larvae of *Diadema setosum*. He states that these animals under certain conditions swim downward in light and move upward in darkness. Acids and alkalies have marked influence upon phototropism. Thus the phenomena already described for certain Crustacea exist not only in animals swimming by muscular movement but also in organisms moving by ciliary action. However, Kanda (1918) states that reversibility of the negative geotropism of *Paramecium* by temperature and by chemicals is extremely doubtful.

Bolin (1926) found that certain rotifers, *Mytilina spinigera* and *Rattulus rattus*, are negatively phototropic to strong as well as to weak light. Carbon dioxide has no influence upon phototropism, but the animals become positively phototropic when hydrogen sulfide is dissolved in the cul-

ture medium. It was also observed that *Mytilina*, *Rattulus*, and *Rotifer neptunius* show positive geotropism under normal conditions, while the reaction is reversed in both light and darkness when carbon dioxide or hydrogen sulfide is placed in the medium surrounding them. No chemotropism exists in these animals. Bolin states that the reactions described harmonize with the natural habits of these animals.

MIGRATION AS AN EFFECT OF PERIODIC CHANGES IN METABOLISM

In discussing the literature, it seems necessary to note another possible explanation. Menke (1911) carried out experiments with *Idothea* and found that chromatophores expand in daytime and contract at night. The periodical change of the chromatophore movement corresponding to the usual periodicity occurs even if the animals are kept in darkness. Such facts are applied by Menke to the diurnal migration of plankton. He states that the periodical migration and the periodicity of the chromatophore movements are essentially of like nature, and are conditioned by periodicity of metabolism. As has been noted, Esterly (1919) pointed out that *Acartia* exhibits a rhythmical change in geotropism that is not connected with the external conditions.

Ewald (1910, 1912) presents another point of view in regard to the causes of diurnal migration. Working with *Daphnia*, *Leptodora*, *Bythotrephes*, *Bosmina*, and the nauplii of *Balanus*, he reached the conclusion that these animals cease their locomotor movements if they come to a region where the light is too intense and therefore they sink down, and they again begin to swim upward when they reach a region of lower intensity of light. Thus the animals maintain themselves in a region of about the same degree of illumina-

tion all day long. They ascend in the evening and descend in the morning without giving phototropic reactions.

Eyden (1925) observed the daily changes in the specific gravity of *Daphnia pulex*. The maximum specific gravity was found in the morning and the minimum in the evening. Eyden states that the changes in the specific gravity may be considered as a factor in the upward and downward movement of *Daphnia*.

In concluding the review of the literature, it is proper to mention the theory of Ostwald. He (1902) states that the descent and ascent of plankton is due to the decrease and increase of the viscosity of water through its increase and decrease in temperature. Further he states that the vertical movement of plankton is not so much due to the tropisms of organisms as it is to the alternation of the viscosity of water. This theory, however, may be applied only to the diurnal vertical movements of organisms which live very near the surface and have only very limited powers of locomotion.

Still another point of view is expressed by Franz (1911, 1912, 1913). He holds that vertical movement does not occur and that animals are really as abundant at the surface during the day as during the night, but that they escape the net when it is light enough for them to see. There is not space to go more fully into this view. Many field observations show apparent diurnal migration of many species of animals in the ocean and in lakes, with the exception of very shallow and turbid ponds, or high mountain lakes.

LIGHT AND TEMPERATURE AT DIFFERENT DEPTHS IN LAKES

When the sunlight passes through the water of a lake or the ocean, it is absorbed until at some depths there is absolute darkness. The intensities of light at dif-

ferent depths of the sea have been measured by various observers. Recently Pool and Atkins (1926-1929) carried out measurements of the submarine illumination in the Plymouth area by means of photo-electric cells. They show that the mean value of the percentages of light in air reaching 5, 10, 15, 20, 40 and 60 meters are 37.3, 23.6, 14.4, 6.62, 0.72 and 0.085 respectively. During the observations a Secchi disc was just visible at depths of 9 to 14 meters. It has also been shown that the visibility of the Secchi disc is independent of the illumination in air within rather wide limits and that the illumination at the depth at which the disc is just visible is around 16 per cent of that in air.

In a lake in the temperate zone the surface temperature rises steadily from the end of March until August, when it reaches a maximum. At this period the temperature of the surface water is generally around 20°C., while at depths of 5 to 15 meters the temperature suddenly falls. This layer of sudden change in temperature is known as the thermocline or mesolimnion. Below this layer or in the hypolimnion the temperature of the water is generally lower than 10°C. In deep lakes the temperature of the bottom water is 4°C. The differences in the intensity of the light as well as in the temperature of the water at different depths must have marked influence upon the vertical movements of plankton.

For making catches of plankton it is most desirable to use the pump method. Water may be pumped up through a hose from various depths and at intervals throughout the day. The water is strained through a plankton net and all the planktons in each catch are counted. Fifty liters of water are sufficient for this purpose. The changes in the vertical distribution of the plankton at different pe-

riods may thus be studied. But if the water is too transparent and the planktonts are found abundantly in a stratum deeper than forty or fifty meters, as in the case of the open ocean, the pump method can not be employed. In this case the vertical and horizontal closing net may be used.

IS DIURNAL MIGRATION DUE TO CHANGES IN LIGHT?

If the diurnal migration of planktonts is due largely to light, as certain earlier investigators maintained, there should be

any observed, *Diaphanosoma brachyurum* was distributed in a stratum ranging from 8 to 12 meters, while in Suigetu Lake, where the water was the most turbid, it predominated from the surface to a depth of 3 meters. The observations made on Kizaki Lake and Lake Biwa show that the more transparent the water is, the deeper the planktonts are found in the daytime. The vertical distributions of other species in Aoki Lake and Kizaki Lake are illustrated in Figures 1 and 2. All plankton crustaceans, such as *Holopedium*, *Polyphemus*, *Bosminopsis*, *Daph-*

TABLE 1

The vertical distribution of Diaphanosoma brachyurum (The number of individuals in each liter is indicated)

	SUIGETU LAKE	KIZAKI LAKE	KIZAKI LAKE	LAKE BIWA	LAKE BIWA	AOKI LAKE	AOKI LAKE
Dates.....	16/IX/26	16/VII/27	11/VIII/25	1/IX/27	10/VII/27	16/VIII/25	20/VIII/27
Time.....	1-2 p.m.	2-3 p.m.	1-2 p.m.	2-3 p.m.	12-1 p.m.	2-3 p.m.	2-3 p.m.
Weather.....	Fine	Fine	Fine	Fine	Fine	Fine	Fine
Thermocline.....	5-10m.	5-12m.	5-12m.	12-20m.	12-20m.	5-12m.	5-12m.
Transparency.....	1 m.	4.5 m.	6 m.	8 m.	12 m.	10 m.	12 m.
0.	8.6	0	0	0	0	0	0
2	10.9	12.6	1.0	1.2	0	0	0
3	12.4
5	2.1	6.9	19.0	10.8	0.3	0.4	0
8	0.1	0.7	...	9.2	4.5
10	0	0	0	7.6	1.2	16.0	15.4
12	0	0	...	1.3	16.4
15	0	0	0	1.2	1.1	0	0
20	...	0	0	0.4	0.4	0	0
25	...	0	0	0.1	0	0	0

a direct relation between the transparency of the water and the depths to which the planktonts descend in the daytime, and there should also be a close relation between changes in the intensity of the sunlight and the vertical movement of plankton, i.e., the upward movement should take place at dusk and at dawn or there should be differences in the vertical distribution on rainy, cloudy, and sunny days.

Table 1 shows that such relations obtained in some Japanese lakes. In Aoki Lake, where the water was the clearest of

nia, *Bosmina*, and *Diaptomus* are found in deeper strata in Aoki Lake than in Kizaki Lake. A similar relation has been noted by Burckhardt (1900) for *Daphnia* in Vierwaldstättersee, but Juday (1903) could not find such a relation for any migrating Crustacea in the Wisconsin lakes.

Some Crustacea are found nearer the surface on cloudy or rainy than on clear days. Birge (1897) made a set of observations on Lake Mendota on a day when there was an alternation of cloud and sun. During the sunny periods, *Daphnia* was found at a depth of one meter and during

the cloudy periods one-half meter. Burckhardt (1900) and Juday (1903) found a similar relation for *Daphnia* and *Diaptomus*. In Kizaki Lake *Bosminopsis*, *Polyphemus*, and nauplii were absent or very few at the surface on clear days but were found there on rainy days in as great abundance as in the evening. Russel

dull days this copepod came nearer the surface.

VERTICAL DISTRIBUTION OF PLANKTON THROUGH THE DAY

Blanc (1898), Fordyce (1900), and Fuhrmann (1900) stated that in their investigations Crustacea reached a maximum of

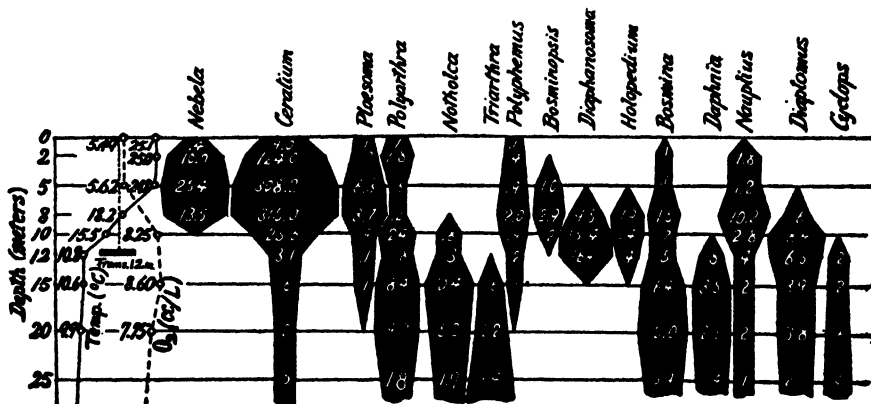


FIG. 1. THE VERTICAL DISTRIBUTION OF PLANKTON IN AOKI LAKE ON AUGUST 20, 1927

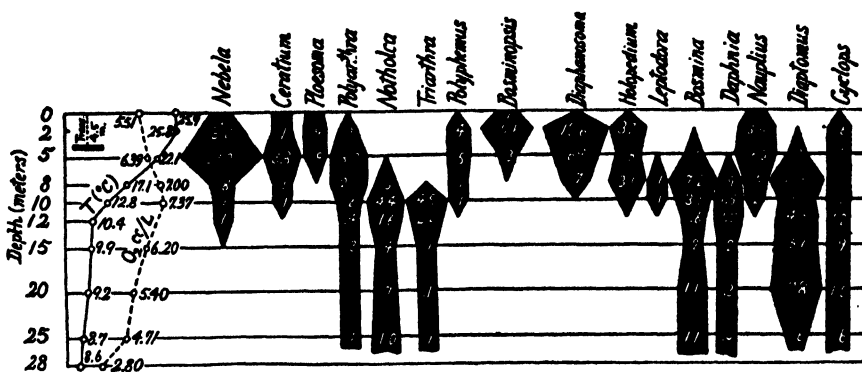


FIG. 2. THE VERTICAL DISTRIBUTION OF PLANKTON IN KIZAKI LAKE ON JULY 28, 1927
(The number of individuals per liter is indicated)

(1926) pointed out that seasonal variations in light intensity as well as the changes due to the weather have important influences upon the vertical distribution of marine plankton. Figure 3 shows that *Calanus finmarchicus* was distributed nearer the surface in April than in June and July on clear days. It can also be seen that on

abundance at the surface shortly before dawn. However, later observations showed that Crustacea are found in greatest numbers at the surface at midnight or in the early hours rather than toward dawn. Ruttner (1905) first pointed out that *Hyalodaphnia Kahlbergensis* reaches a maximum of abundance at the surface twice

during the day, at dawn and at dusk. He called the type of migration with one maximum at night "nocturnal migration" and that with two maxima at dawn and at dusk "twilight migration."

tion changes. During the day the sun shone brightly. In evening the light gradually faded until the sun sank below the mountains at 5.30 p.m. The sun set at 6.30 p.m. After sunset the light suddenly

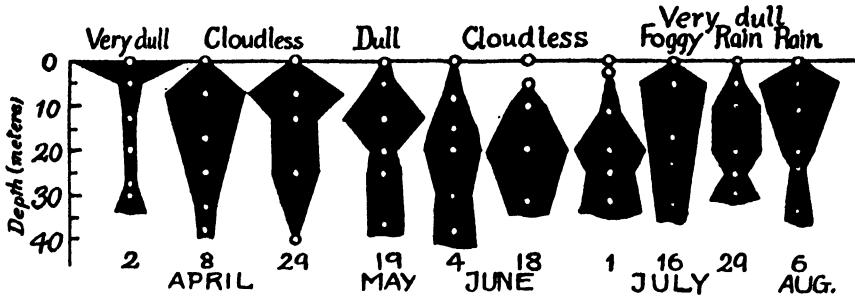


FIG. 3. THE VERTICAL DISTRIBUTION OF *CALANUS FINMARCHICUS* IN THE PLYMOUTH AREA ON DIFFERENT DAYS (AFTER RUSSEL)

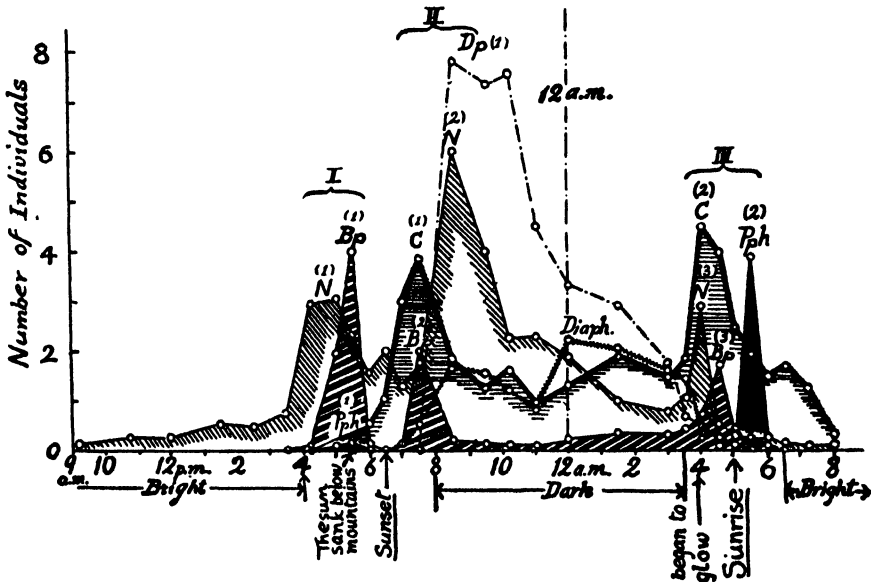


FIG. 4. THE VARIATION OF THE NUMBER OF INDIVIDUALS AT THE SURFACE OF KIZAKI LAKE ON AUGUST 6-7, 1929 (The number of individuals per liter is indicated). N. = Nauplius, Bp. = Bosminopsis, Pph. = Polyphemus, Diaph. = Diaphanosoma, C. = Cyclops, Dp. = Diaptomus

Figure 4 shows the variation in the number of individuals at the surface of Kizaki Lake at hourly or at half-hourly intervals throughout a day and a night. Before examining the curves it is necessary to bear in mind the times at which the illumina-

began to decrease and from 8 p.m. to 3.30 a.m. it was dark and there was no moon. At 4 a.m. the eastern sky began to glow and at 5.00 a.m. the sun rose. At 5.30 a.m. the sun threw the first beam upon the lake. From these descriptions it is clear that

there were three periods of changing intensity of sunlight; in the evening, after sunset, and at dawn. In examining the curves it is apparent that the upward movement of the plankton takes place when the light intensity changes. At the first period of change in illumination, or a few hours before sunset, nauplii, *Bosminopsis* and *Polyphemus* appeared at the surface. Later there was a tendency to swim downward. At the second period, or during a few hours after sunset, the maxima of abundance for nauplii, *Bosminopsis*, *Cyclops*, and *Diaptomus* were found. After 10 p.m. the number of the Crustacea in

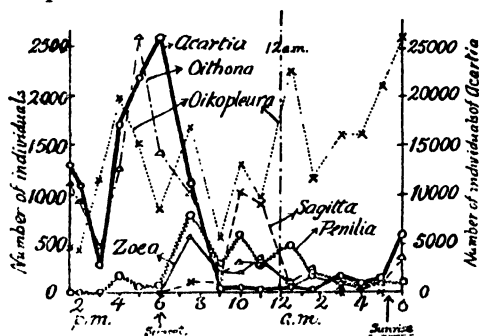


FIG. 5. THE VARIATION OF THE NUMBER OF INDIVIDUALS AT THE SURFACE OF HIRUGA LAKE ON SEPTEMBER 18-19, 1926

(The number of individuals per cubic meter is indicated.)

the plankton suddenly decreased, and at 3.30 a.m., shortly before dawn, the fewest were found. At the third period, or at dawn, the nauplii, *Bosminopsis*, *Polyphemus* and *Cyclops* came up to the surface. Nauplii and *Bosminopsis* had three maxima, and *Cyclops* and *Polyphemus* had two. These animals belong to the class of twilight migrators and seem to afford good evidence that their daily vertical movements are due largely to changes in light intensity. *Diaptomus* and *Diaphanosoma* had only one maximum. They afford examples of nocturnal migration. The frequency of appearance at the surface

seems to be closely related to the depth at which planktons are distributed in the daytime. Animals distributed in the surface layer during the day have three maxima and those found in the deeper layers have two or one. The relations will be seen in Figure 1.

Esterly (1912) and Russel (1925, 1926, 1928) showed that the maximum number of individuals of the marine plankton Crustacea at the surface is found in the early hours of the night, as is the case for the freshwater Crustacea (Fig. 5 and 6).

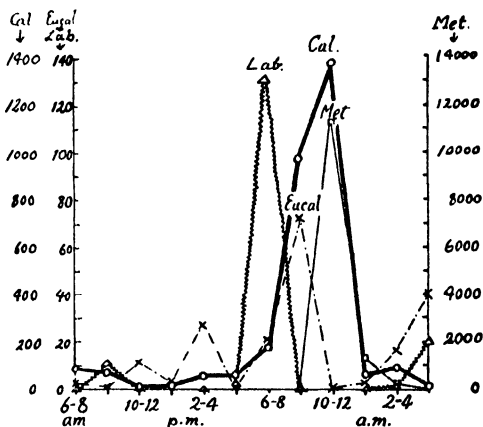


FIG. 6. THE VARIATION OF THE NUMBER OF INDIVIDUALS AT THE SURFACE OF THE SAN DIEGO REGION ACCORDING TO TIME OF DAY

(The number of individuals per hour is indicated.)
Cal. = *Calanus*, Eucal. = *Eucalanus*, Lab. = *Labidocera*.
Met. = *Metridia*.

It is worthy of notice that *Acartia*, in which the physiological rhythm was observed by Esterly, came up to the surface a few hours before sunset and most individuals left the surface one hour after sunset. *Calanus*, *Metridia*, *Eucalanus*, *Penilia*, *Evadna*, *Sagitta*, and other marine planktons tend to move downward at later hours.

TYPES OF DIURNAL MIGRATION

If the variation in the vertical distribution of plankton according to the time of

day is kept in mind the whole problem of migration will be clearer. There are various types of diurnal migration. Some species actually congregate at the surface at night and leave the lower water, while others merely move up into the surface layer at night; in these there is no change in the distribution of the lower water, so that they become evenly distributed from the surface downward. In some animals

tribution of the Crustacea within one half meter of the surface, while below three meters the movement was very slight. The same was observed by Zieglmeyer (1927) in the Tegersee. Juday (1903) made observations on ten of the lakes of Wisconsin. In three of them the migrations were confined within these narrow limits, but in the other seven lakes, the change in the vertical distribution ex-

TABLE 2

Polyphemus pediculus. The vertical distribution in Kizaki Lake on August 12-13, 1925. (In tables 2-14, the number of individuals per liter is indicated)

DEPTH (meters)	1.00 P.M.	6.30 P.M.	10.00 P.M.	1.00 A.M.	5.30 A.M.
0	0.1	4.0	0	0.1	2.6
2	2.0	1.6	0.2	0.2	0.6
5	0.4	0.6	1.2	1.4	1.0
10	0	0.1	2.0	1.8	0.3
15	0	0	0.1	0	0
20	0	0	0	0	0

TABLE 3

Bosminopsis deitersi. The vertical distribution on July 28-29, 1927, in Kizaki Lake

DEPTH (meters)	1.00 P.M.	7.00 P.M.	9.45 P.M.	12.30 A.M.	3.30 A.M.	5.00 A.M.
0	0.1	1.5	0.1	0.2	0.4	0.7
2	5.6	1.8	0.1	0.3	1.0	5.5
5	0.3	0.5	0.2	2.1	0.5	0.4
8	0
10	0	0.6	0.9	0.7	2.0	1.0
12	0
		0	0	0	0	0

the distribution in daylight is somewhat modified at night but only a few individuals move up to the surface layer. There are still other types of migration. Some forms show a tendency to move upward at night but do not reach the surface layer, and others show no change in their vertical distribution throughout the day and night.

In Wisconsin Marsh (1900) observed the most marked change in the vertical dis-

TABLE 4

Diaphanosoma brachyurum. The vertical distribution in Kizaki Lake on July 28-29, 1927

DEPTH (meters)	1.00 P.M.	7.00 P.M.	9.45 P.M.	12.30 A.M.	3.30 A.M.	5.00 A.M.
0	0	19.4	22.9	19.0	11.8	0.5
2	12.6	28.0	23.0	20.0	21.6	13.0
5	6.9	8.0	9.2	8.6	10.4	18.0
8	0.7
10	0	0.1	0.1	0.2	0.6	0.6
12	0
15	0	0	0	0	0	0

TABLE 5

Diaphanosoma brachyurum. The vertical distribution in Aoki Lake on August 20-21, 1927

DEPTH (meters)	1.00 P.M.	7.30 P.M.	10.10 P.M.	2.00 A.M.	5.30 A.M.
0	0	6.0	18.0	7.8	0
2	0	5.5	19.0	8.3	0
5	0	20.5	17.5	22.3	0.2
8	4.5
10	15.4	12.5	0.6	6.5	10.5
12	16.4
15	0	0	0	0	0

tended to deeper strata. Further he states that the movement of any species rarely affected the vertical distribution more than three or four meters below the upper limit in the daytime. Burckhardt (1900) observed the definite migration of Crustacea to the surface in Vierwaldstättersee. He showed that the plurimum of *Daphnia hyalina* was found in 20 to 60 meters in the daytime but at night was between 0 and 10 meters. *Leptodora* had a range 10 to 40

meters during the day and 0 to 10 meters at night. Tables 2 to 7 show the changes of the vertical distribution of various plankton Crustacea at different periods of the day. Tables 2 and 3 show the twilight migration. The upward movement is clearly shown in the vertical distribution at 6.30 p.m. and 5.30 a.m. in Table 2 and at 7.00 p.m. and 5.00 a.m. in Table 3. The downward movement at night was so remarkable that the plurimum was found at a depth of five to ten meters, where only a few animals were found in the daytime.

Tables 4-7 give examples of nocturnal migrations. Tables 4 and 6 show that

cal movements seem to be more extensive in transparent than in turbid lakes.

Russel (1925, 1926, 1928) showed that not only the Crustacea of the plankton but certain medusae, polychaete larvae and fish larvae perform definite migrations to the surface. Esterly (1912) showed that the Copepoda were distributed in deeper strata in the San Diego region than the Plymouth area, and as a result the extent of the vertical movements was greater.

Birge (1895) and Juday (1902) state that the diurnal migration of the plankton Crustacea was not affected by moonlight

TABLE 6

Diaptomus pacificus. The vertical distribution in Kizaki Lake on July 28-29, 1927

DEPTH (meters)	2.00 P.M.	7.00 P.M.	9.45 P.M.	12.30 A.M.	3.30 A.M.	5.00 A.M.
0	0	0	1.8	3.0	0.4	0
2	0	0.1	1.9	4.2	1.3	0
5	0.2	2.5	4.5	3.8	3.4	0.1
8	10.8
10	7.1	9.8	8.5	11.1	5.9	9.6
12	4.3
15	5.1	7.9	4.3	6.6	7.9	7.9
20	7.8	6.9	8.0	7.3	8.8	8.2
25	0.6

TABLE 7

Diaptomus pacificus. The vertical distribution in Aoki Lake on August 20-21, 1927

DEPTH (meters)	2.00 P.M.	7.30 P.M.	10.10 P.M.	1.00 A.M.	5.30 A.M.
0	0	0	15.8	6.0	0
2	0	0	11.8	5.3	0
5	0	0.5	6.6	7.8	0.1
8	0.6
10	20.2	17.2	8.3	7.3	23.0
12	6.3
15	3.9	6.8	5.7	6.1	7.7
20	3.8	3.4	7.4	5.7	5.3
25	2.5

the amount of the movement of *Diaphanosoma* and *Diaptomus* was very slight in a layer three to five meters below the upper limit of the day distribution in Kizaki Lake. But in tables 5 and 7, the same species show more marked movements in Aoki Lake. There was a general upward movement of the whole mass of the animals. The plurimum of both species had a range of from ten to twelve meters deep during the day, while at night only a small part remained in that stratum; the great majority moved upward and were found from the surface to a depth of five meters. In general, the diurnal verti-

cal movements seem to be more extensive in transparent than in turbid lakes. Russel (1926) found that certain animals, especially fish larvae, showed a more marked movement upward on moonless than on moonlight nights.

THE EFFECT OF THE THERMOCLINE

The vertical movements of *Diaptomus*, *Cyclops*, *Diaphanosoma*, *Holopedium*, *Bosmina*, some species of *Daphnia*, *Polypheum*, and almost all marine planktonts seem not to be affected by the thermocline or the changes in temperature of water. However the migrations of some species show noteworthy exceptions.

Juday (1903) found *Limnocalanus macrurus* distributed in the daytime below a depth of fifty meters in Green Lake. It began to move upward at night, but when it reached the thermocline, further upward movement was clearly retarded. Juday made similar observations on *Daphnia longiremis* in Okauchee Lake, *D. pulicaria* in Lake Mendota and in Winona Lake, *D. retrocurva* in Lake Mendota, and *D. hyalina* with round helmet in Rainbow Lake. Birge (1897) was also unable to

tendency to move upward at night, but not a single individual was found above a depth of five meters or in the epilimnion at night (Table 9). However, *Daphnia longispina* came up near the surface in winter when the temperature of the surface water decreased (Table 8).

There are still other types of diurnal migration which seem to be affected by the thermocline. In the first type, the depth to which the animals descend in the daytime does not depend upon the intensity of

TABLE 8

The vertical distribution of Daphnia longispina, illustrating the effect of the thermocline

Lakes..... Dates..... Thermocline...	Kizaki L. 11/VIII/25 5-12m.	Kizaki L. 26/VII/27 5-12m.	Aoki L. 16/VIII/25 5-12m.	Aoki L. 20/VIII/27 5-12m.	L. Biwa 6/X/26 12-20m.	Noziri L. 20/VIII/28 12-15m.	Kizaki L. 5/XII/25 15-20m.	L. Mendota Aug. 1895 (Birge)
0	0	0	0	0	0	0	0.1	0
2	0	0	0	0	0	0	0.3	0
5	0	0	0	0	0	0	0.5	
8	...	0.9	...	0	0	0	...	11.0
10	10.4	1.5	1.2	0	0	0	0.5	65.0
12	...	1.2	...	0.8	...	0	...	22.0
15	7.0	0.2	1.8	3.5	0	0.1	0.5	1.6
20	0.1	0.3	0.8	2.6	0	0.1	0.2	
25	0.1	0.3	0.5	1.4	0.2	...	0.1	
30	0.1 (28m.)	...	0.2	...	0.8	...	0 (28m.)	

find a diurnal migration of *D. pulicaria* in Lake Mendota. The effect of the thermocline upon the vertical distribution of *D. pulicaria* is more clearly shown when the seasonal changes in vertical distribution are studied (Birge, 1897; Juday, 1903). Juday noted, for instance, that the thermocline was two meters deeper in October than in August in Oconomowoc Lake and the day position of *D. pulicaria* was likewise found two meters deeper. About the middle of June it was found much nearer the surface.

In Japanese Lakes *Daphnia longispina* is generally distributed below the thermocline (Table 8). It apparently shows a

TABLE 9

The vertical distribution of Daphnia longispina in Aoki Lake on August 20-21, 1927

DEPTH (meters)	TEMPERATURE	1.00 P.M.	7.30 P.M.	10.10 P.M.	1.00 A.M.	5.30 A.M.
0	25.1	0	0	0	0	0
5	24.8	0	0	0	0	0
8	18.2	0
10	15.5	0	0.2	6.5	4.2	0.8
12	10.8	0.8
15	10.6	3.5	5.5	4.5	6.0	9.0
20	9.9	2.6	2.3	4.0	3.8	6.8
25	9.1	1.4

the sunlight. Plankton occupy the lower part of the mesolimnion on cloudy as on

sunny days. However, during the upward movement at night there is no evidence of influence of the thermocline. For example, *Epischura* and *Leptodora* in Winona Lake and *Mysis relicta* in Green Lake and Trout Lake are found in the lower part of the thermocline and do not change the day position on cloudy as on clear days, while they were found in surface catches at night (Juday, 1902, 1927). In another case, the thermocline apparently prevents the downward movement of the animals in the daytime. Birge (1897) states that in Pine Lake and Oconomowoc Lake, in both of which many Crustacea range through the thermocline, *Diaphanosoma* is confined to the region above it. March (1897) found that *Epischura* had a similar distribution in Green Lake.

DIURNAL MIGRATION IN WINTER

As the thermocline has a marked influence upon the vertical movements of planktons, it would be expected that the diurnal movement in winter would differ from that in summer. The planktons are distributed evenly in winter from the surface downward and the upper limit of the distribution is found very much nearer the surface, owing to the weakness of the intensity of the sunlight and to the circulation of the water by strong winds. As a result diurnal vertical movements are found only in exceptional cases.

In Kizaki Lake, with the exception of an apparent migration of adult *Diaptomus*, it was impossible to detect any vertical movement of the plankton Crustacea on December 5 (Table 10).

When the lake is covered by ice, the water again becomes stagnant. During this period zonal vertical distribution is found as in the case of the summer period of stagnation. But when the ice is covered with snow the lake becomes dark even

at the surface layer. Then the animals are distributed evenly from the surface downward. Ruttner (1909) showed that *Diaptomus* was more uniformly distributed in the Grösser Plöner See when the ice was covered with snow (Table 11). Behrens (1914) found an apparent diurnal migration of the Copepoda under the ice covering in Sakrower See. The maximum of

TABLE 10

The vertical distribution of adult *Diaptomus pacificus* in Kizaki Lake on December 5, 1925

DEPTH (meters)	TEMPERATURE	12 M.	4 P.M.	10 P.M.
0	8.2	0.4	0.1	2.0
2	8.3	0.9	1.2	1.8
5	8.2	1.3	1.1	2.0
10	8.2	0.4	1.1	0.7
15	8.1	0.9	1.3	0.6
20	6.7	0.7	1.5	0.4
25	5.6	0.4	0.5	0.2
28	5.6	0	0.1	0

TABLE 11

The vertical distribution of *Diaptomus* in Grösser Plöner See, illustrating the vertical distribution under the ice covering with and without snow (After Ruttner)

DEPTH (meters)	JAN. 20, 1909 ICE..... 10 CM. SNOW..... 0 CM.	FEB. 13, 1907 ICE..... 25 CM. SNOW..... 9 CM.
0	0.3	4.4
2	11.0	4.1
5	11.0	4.3
10	1.6	3.6
20	0.6	2.5
30	4.5	5.4

abundance at the surface was found at midnight (Table 12).

DIFFERENCES IN DIURNAL MIGRATION BETWEEN ADULTS AND YOUNG

The difference in the vertical distribution and the diurnal migration between adult and young Crustacea has been observed by various workers. Birge (1897) found in Lake Mendota that young *Daph-*

nia predominate in the higher levels over the adults. Burckhardt (1900) and Juday (1903) made similar observations on *Daphnia* and Kikuchi (1927) on *Diaptomus*

and found further that the young usually reach the surface earlier in the evening and remain there later in the morning than the adults. Table 13 shows the vertical dis-

TABLE 12
Vertical distribution of copepods in Sakrower See on February 23-24, 1912. (After Behrens)

DEPTH (meters)	1.30-3 P.M.	5-6	7-8	10.30-11.30	1 A.M.- 2.30	4-5	6-6.30	7-8	8-8.30	1-2 P.M.
0	0	2.1	28.1	95.0	138.0	36.0	25.3	12.6	1.3	0.1
1	5.2	1.8	5.6	45.0	81.0	33.0	33.2	8.6	1.9	0.1
3	...	4.8	6.4	26.7	60.0	16.6	11.8	10.8	3.6	1.9
5	7.3	4.2	9.2	17.1	27.2	14.2	15.2	16.7	8.3	1.6
10	2.5	3.0	15.4	8.8	5.4	7.6	...	15.0	6.0	3.2
15	4.2	6.6	10.3	2.6	5.1	5.8	...	9.6	...	4.2
20	8.6	8.5	8.7	5.2	3.8	4.6	...	10.0	...	4.0
25	10.8	19.3	8.2	5.7	2.9	3.9	...	5.2	...	3.6
30	19.1	17.4	9.7	4.4	4.9	3.0	...	5.1	...	7.2
33	61.0	73.0	89.0	34.0	78.0	17.0	...	9.0	...	16.0
35	60.0

TABLE 13
Vertical distribution of *Diaptomus pacificus* in Kizaki Lake
at 2 p.m. on August 12, 1925
Naup. = Nauplius, Y.1. = Young, 0.4-0.5 mm. long,
Y.2. = Young, 0.55-0.65 mm. long, Y.f. = Young
female, 0.75-0.9 mm. long, A.f. = Adult female,
1.2 mm. long, Y.m. = Young male, 0.8-0.85 mm.
long, A.m. = Adult male, 1 mm. long

DEPTH	NAUP.	Y. 1.	Y. 2.	Y. F.	Y. M.	A. F.	A. M.
0	0.1	0	0	0	0	0	0
2	0.5	0.1	0	0	0	0.1	0
5	4.0	0.1	0	0	0	0.1	0.1
10	2.4	4.4	3.6	1.6	0.3	1.6	2.8
15	0.3	0.6	2.8	2.0	0	2.8	0.2
20	0	0	0	0.4	0	0.3	0
25	0	0	0	0.1	0	0	0
28	0	0	0	0	0	0	0

tribution of young and adult *Diaptomus* in Kizaki Lake in the daytime. Table 14 shows the time at which the young and adults reach the surface in the evening and leave there in the morning in Kizaki Lake.

On the basis of laboratory experiments Dice (1914) pointed out that the young of *Daphnia* showed more strongly marked positive phototropism and negative geotropism than the adults. Rose (1925) also observed that the young *Daphnia* exhibited a decided positive phototropism while the oviparous females showed negative phototropism. These reactions may probably tend to cause the young to be found nearer the surface than the adults. On the other hand, Southern and Gardiner

TABLE 14
The change of the number of individuals of *Diaptomus pacificus* at the surface layer in Kizaki Lake on August 6-7, 1929

	6.30 P.M.	7.00	7.30	8.30	9.30	1.30 A.M.	3.00	3.30	4.00	4.30	5.00
Naup.....	2.0	1.3	1.7	6.0	4.1	1.0	0.8	1.1	2.9	0.5	0.3
Young.....	0	0	0.2	3.7	6.3	2.1	1.5	0.5	0.3	0.1	0
Female.....	0	0	0	2.4	0.7	0.4	0.2	0.1	0	0	0
Male.....	0	0	0	1.6	0.4	0.4	0.1	0.1	0	0	0

(1926) found in Lough Derg that the adults of *Daphnia hyalina* were distributed in a higher level by day than the young and that the latter made a greater vertical movement than the adults. In Kizaki Lake the nauplii of *Cyclops* were found near the bottom, while the adults were distributed in the upper strata.

Russel (1928) states that the vertical distribution appears to differ for the two sexes of *Calanus finmarchicus*, the males tending to avoid the surface layer more than the females. The freshwater Copepoda seem to show no marked difference in the vertical distribution of the two sexes.

IRREGULARITIES IN DIURNAL MIGRATION

The type of diurnal migration shown by each species is fairly uniform from day to day in each lake, though the actual depth may vary, owing to changes in the intensity of the sunlight or in the transparency of the water. In some species, however, irregularities have been observed. Juday (1903) states that *Daphnia hyalina* with round helmets showed no diurnal migration in Rainbow Lake, that those with pointed helmets did, while the reverse of this was true in Okauchee Lake, and there was a movement of both varieties in Naga-

wicka Lake. *Daphnia pulicaria* remained in cold water in Lake Mendota and showed no vertical movement, but in Oconomowoc Lake and in Okauchee Lake the same species apparently made a diurnal migration extending through twelve meters.

The writer found that *Holopedium gibberum* showed an apparent movement in the summer of 1925 and 1927 in Kizaki Lake, but no movement was observed in 1929 in the same lake nor in Aoki Lake in 1927. *Cyclops strenuus* was distributed below the thermocline and showed no movement in Kizaki Lake in 1925, but in 1927 in the same lake and in Aoki Lake it was distributed evenly from a depth of two meters downward and showed a diurnal migration. Whether the causes of the irregularities in the vertical distribution and diurnal movement are to be found in internal or external factors is not certain. But the facts presented show that the diurnal migration is changeable in the lakes.

The diurnal migration of diatoms, flagellates, Protozoa, Rotatoria, and other organisms which have very weak locomotor activity has been observed, but the extent of the movement is confined within narrow limits. *Ceratium* and *Anuraea* make somewhat extensive movements.

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PHENOLOGY AND ONE OF ITS MODERN DESCENDANTS

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*Contribution from the Zoological Laboratories, University of
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FOR savage and uncivilized man the flowering of certain plants and appearance of certain animals must have been an important guide to hunting, fishing, fruit gathering and primitive agriculture. The time of flowering and fruiting of various plants is still an important guide to many agricultural operations. Part of the work of several important weather stations still consists in recording the status of certain flowering plants, grown for the purpose of adding biological data to that obtained from instruments.

Calendars of periodic events have been used in connection with agricultural practice for thousands of years. Becquerel (1853) describes several calendars. A Chinese calendar of 700 B.C. does not differ essentially from some spray calendars of twenty-five years ago. According to this Chinese calendar, swallows arrive in the Hoang Ho Valley from the 9th of April to the 8th of May. According to a Roman calendar of 45 A.D. they arrive in Spain the 21st to 28th of February. The Chinese and Roman calendars were compared with a Moorish calendar for Spain of 961 A.D. which recites the agricultural operations and periodic events of each month. Becquerel also discusses a calendar for Spain of 1551 and was able to draw some general conclusions from these several in accord with his own observations and those of other European workers. In the first half of the nineteenth century attention appears to have centered upon a

generalization as to the relations of a given periodic event, as for example the flowering of a particular widely distributed plant, or appearance of a particular animal to altitude and latitude. Thus in 1830 according to Hopkins (1918) Schubler found that between Parma, Italy, and Greifswald, Prussia, periodic events were later in spring by four days for each degree of latitude and for each 100 meters of altitude. Hopkins finds also that Fritsch stated a similar principle in 1866. Hopkins' own work is applied to the prediction of the dates free from infesting stages of the Hessian fly. His work is, however, directly descended from the earliest type of observation, carried on without thermometers or other instrumental studies.

RÉAUMUR AND THE SUMS OF TEMPERATURES

The line of particular investigation with which we are concerned represents a series of ideas which grew out of the use of the thermometer and other instruments in connection with observations of periodic events in plant and animal communities. It is, therefore, an offshoot from the series of researches which we have discussed above. The rain gage was early used, but effective work with temperature awaited Galileo's invention of the hermetically sealed alcohol instrument about 1612 A.D. This was commonly known as the Florentine thermometer, and one scale division represented one thousandth of the volume of the lower bulb, the zero being essen-

tially the upper limit of the bulb. The series of studies with which we are concerned evidently began with the observations of the thermometer by M. de Lahire, astronomer and famous member of the Academy of Science of Paris, who published observations of heat and cold for the year 1696 in *l'Histoire de l'Academie* for that year. At the death of M. de Lahire in 1718 the observations were continued by M. Yaraldi, his nephew. He was followed by the illustrious naturalist Réaumur, who recognized that the temperature observations of that period lacked fixed points or standards to make them comparable. He therefore used the freezing point of water, as Newton and Fahrenheit had already done, for the starting point. He marked this 0 and made each scale division represent $1/1000$ of the volume of alcohol in the bulb and tube below his zero. It happened that with the quality of alcohol which he used, water boiled at 80° . In 1735 he published a considerable series of readings of the thermometer taken in the morning at about 6 o'clock and about 2 o'clock in the afternoon. On page 746 he states the sums of mean daily temperatures for April, May, and June—the months in which grain and grapes make their principal growth. He compares 1734, a year with large sums of temperature, with 1735, a year with small sums, and points out a half month's difference in the maturation of fruit and grain. He advocated the use of the sums of mean daily temperatures in comparing different climates and estimating the time of maturing of plants.

During the century following Réaumur's first publication on this subject, Becquerel states that several investigators carried on observations from the same point of view as Réaumur but differed as to method of determining the sum of mean temperatures. He refers, however, to de Candolle,

who began his work a century after Réaumur, as having a different point of view. The latter advocated the use of the temperature at which a plant *begins development* as the starting point from which the sum should be computed. De Candolle was probably the first to introduce experimental work into this field. He determined the minimum temperature for the germination and growth of different seeds.

OETTINGEN AND THE THRESHOLD OF GROWTH

One of the outstanding investigations of the last half of the preceding century is that of Oettingen (1879), who wrote on Dorpat woody plants. He was doubtless influenced by the German psychologists of his time who were developing the idea of the *threshold of stimulation*. The threshold is a statistical point representing the average minimum stimulus giving a perceptible response. Oettingen did not follow the ideas of Weber as represented in Weber's Law, which has usually been interpreted as a logarithmic relation between stimulus and response, but he was probably first to apply the term *threshold* to that temperature just above which development becomes barely perceptible, and to use this temperature on the assumption of a direct proportionality between temperature and rate of development above the threshold.

In other respects he followed the suggestions embodied in Réaumur's summing of temperature and in the experiments of De Candolle on wheat and other plants. The latter found that the threshold for growth is $6^{\circ}\text{C}.$, which has formed the base used by Merriam (1894) in working out his life zones. This is also the base commonly used by meteorologists. The summing of temperature above this base has become a regular practice in the British Meteorological Service for the grain growing districts

of Great Britain. General Strachey (1887) devised mathematical formulae for deriving the sum above 43°F. or 6°C. when only maxima and minima are given. A sum of temperatures above such a mini-

TABLE 1

	10 A.M. 7°C.	11 A.M. 8°C.	12 M. 8°C.	1 P.M. 10°C.	2 P.M. 8°C.	3 P.M. 7°C.	4 P.M. 6°C.
Effective degrees..	1	2	2	4	2	1	0

Sum = 12° C.

mum should be taken by one hour or by two hour periods. If 6°C. is assumed as a threshold, temperatures below this are not supposed to produce any growth or development. The ordinary early spring day will not pass 6°C. before 10 A.M. and will fall below 6°C. about 4 P.M. For ordi-

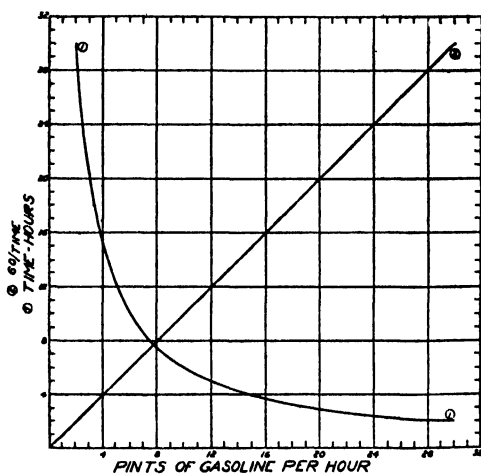


FIG. 1. SHOWING THE RELATIONS OF AN AUTOMOBILE UNIFORMLY CONSUMING ONE PINT OF GASOLINE PER MILE, TRAVELING SIXTY MILES, TAKEN FROM TABLE 1

Showing the equilateral hyperbola formed by plotting time to go 60 miles and pints of gasoline on coordinates. The straight line is the reciprocal of time multiplied by sixty, the constant distance, and plotted on pints of gasoline per hour. The angle between the two axes is divided into two of 45° each. This is the relation assumed in summing temperatures. One pint of gasoline corresponds to one degree above the temperature threshold, i.e., one degree of effective temperature.

nary purposes, when using hour units it is sufficient to subtract 6° from each hourly reading above 6° and ignore the rest; thus with the records in table 1, the sum for the seven hours is 12 hour degrees.

The remaining temperatures, being below 6°C., are ignored and to secure degree days it is necessary to divide 12 by 24 which gives 0.5°C. degree days.

Various Europeans have carried on careful critical studies, employing various detailed methods of determining the total accumulated temperature necessary to bring a given plant into bloom, or to ripen a crop of grain. This total, however, was found to vary for the same stage of development of the same variety of plant from

TABLE 2

Determination of the alpha value by the Oettingen method

TEMPERATURE °C.	HOURS TO COMPLETE DEVELOP- MENT	ALPHA 13° PRODUCT	ALPHA 11° PRODUCT	ALPHA 15° PRODUCT
16	833.3	2499.0	4166.0	833.0
18	500.0	2500.0	3500.0	1500.0
23	250.0	2500.0	3000.0	2000.0
28	166.6	2499.0	2832.0	2165.0

season to season. It has, however, served as an important general guide. Phenology and temperature summing met with the most unreasonable denunciations of plant physiologists of the recent past and, as Oettingen (1879) has said, they merely destroyed but provided nothing better.

THE TIME-TEMPERATURE CURVE

The mathematical relations of the concept of sums are very simple; the assumption is that the time-temperature curve for any biological process is an equilateral hyperbola as shown in figure 1. The product of the ordinate and abscissa establishing any point is a constant. If an organism obeyed this law fully in its temperature

relations there would be a true *thermal constant* often erroneously mentioned in this connection. This would be the time multiplied by degrees above the threshold temperature. That the simple mathematical relations, belonging to a temperature response which Oettingen assumed, were understood is indicated by his method of determining the threshold. He merely assumed thresholds (α values) (See Table 2) and found the products of time and temperature above them. The one which gave the most nearly constant product for all localities and years was regarded as most nearly correct. When the threshold is too low the products decrease as the temperature is higher and when the

in fig. 1.) Rate of travel, which is directly proportional to the reciprocals, may be substituted for them. In this case it is, for example, 60 times the reciprocals or miles per hour.

In the case of development, temperature above the threshold has been used in the place of gasoline and is assumed to be directly proportional to the rate of development. Reibisch (1902) was one early investigator to take advantage of this in calculating supposed thresholds using the so-called straight line equation;— $XY = K$, hence $\frac{K}{Y} = X$. The threshold temperature is *unknown*, but if the temperatures in degrees centigrade are *known* in a few cases,

TABLE 3
Automobile going 60 miles at various speeds

	TIME							
	2 hours	3 hours	4 hours	5 hours	6 hours	10 hours	12 hours	30 hours
Reciprocals of time.....	0.50	0.33 $\frac{1}{3}$	0.25	0.20	0.16 $\frac{2}{3}$	0.10	0.08 $\frac{1}{3}$	0.033 $\frac{1}{3}$
Miles per hour (60 \times reciprocals).	30	20	15	12	10	6	5	2
Pints of gasoline used per hour...	30	20	15	12	10	6	5	2

threshold is too high they increase. Thirteen degrees is the correct value in table 2.

Relative velocity is always expressed by the reciprocal of the time to do a definite amount of work or travel a definite distance. If we assume that an automobile which uniformly uses one pint of gasoline per mile goes 60 miles at various rates of speed, and let gasoline consumed take the place of temperature we have a complete parallel to the assumptions of temperature summing.

The product of time and gasoline gives a constant, the total distance, namely 60, and if the two are plotted as in figure 1 they given an equilateral hyperbola. If the reciprocals are plotted on gasoline used they fall in a straight line (See line 2

the supposed threshold may be determined. Reibisch, who worked on fish eggs, used the symbol α for the unknown point on the scale at which he assumed there was no development. Hence

$$X - \alpha = \frac{K}{Y}$$

or

$$(X - \alpha) Y = K.$$

Taking table 2,

$$X = 18^{\circ} \text{ and } Y = 500 \text{ hours}$$

$$X = 23^{\circ} \text{ and } Y = 250 \text{ hours,}$$

and by substitution in the formula

$$(18 - \alpha) 500 = K \text{ or } 9000 - 500 \alpha = K$$

$$(23 - \alpha) 250 = K \text{ or } 5750 - 250 \alpha = K$$

$$3250 - 250 \alpha = 0$$

$$250 \alpha = 3250$$

$$\alpha = 13$$

Reibisch believed the results calculated in this manner were correct thresholds.

THE WORK OF KROGH

It remained for Krogh (1914), the Danish physiologist, to discover that the zero of the hyperbola or the α of Reibisch is not the threshold of development. He discovered this in working on the rate of development of fish eggs; but made an especial investigation to determine the form of the velocity of development curve using the time to complete the first cleavage plane in the frog's egg. He found that development goes on at the threshold value calculated from experiments at medial temperatures though the rates at the medial temperatures fall into a straight line which passes through their calculated α or threshold of Reibisch. He further found that the rate falls off rapidly at high temperatures, a fact brought out by Lebenbauer (1914) in the Indian corn plant (Curve similar to fig. 4).

It is interesting to note that in the same paper in which Krogh made the leading contribution to this very old concept, he also called attention to the fact that Van't Hoff's rule—a rise of 10° doubles the rate of reaction—does not hold good and is useless as a comparison. He, however, used Arrhenius' (1916) formula, a later developed law of chemical reaction. It appears that the laws of chemical reactions apply to metabolic processes when digestion of food and all activity are eliminated as in insect pupae or in animals under anaesthetics, especially after a correc-

tion is made for the circulatory and respiratory movements. According to Krogh, (1916) basal metabolism is about 75 per cent—a typographical error in Shelford ('29) made this read 25 per cent instead of 75 per cent—of the usual metabolism at 20°C . uncorrected for the involuntary muscular activities. Thus it appears that normal development with activity and feeding follow the law we are describing (Fig. 4 is typical), while standard metabolism, which is basal metabolism at different temperatures, approaches the formula of Arrhenius. Thus, as usual when scientists disagree, they are talking about different things. A decrease in rate at high temperatures is, however, evident in both standard metabolism and the metabolism of normally active animals.

This decrease in rate of development at the higher temperatures was the greatest stumbling block to success with summing temperatures. This is due to the fact that in the case of most plants and animals in the regions where summing was done, any later spring or summer day has several hours in this range of retarded rate. In the course of his study of the codling moth, Glenn (1922) found that the length of the pupal period could not be reduced below a certain minimum, but if the weather became abnormally hot its length was even increased instead of decreased. This led to summing temperature with a correction for retardation. Glenn subtracted twice the hourly temperature above 29.5° from the total degrees for the day taken by hourly means. The velocity of development curve usually assumed in summing is shown in figure 2, while that used by Glenn is shown in figure 3. His assumption was that the velocity decreased at the same rate it had increased. This gave him sums of temperature for the codling moth stages which were far more nearly uniform for the different seasons than

those obtained by the usual method (Simpson, 1903).

Krogh's work showed that for the pupa of the mealworm, an essentially constant amount of CO_2 is given off per unit weight

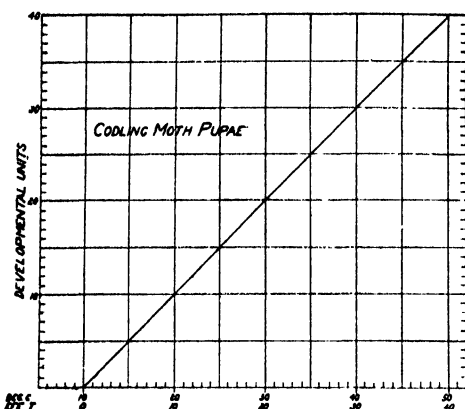


FIG. 2. SHOWING THE RELATIONS ASSUMED BY SIMPSON IN SUMMING TEMPERATURES FOR THE CODLING MOTH

A direct relation between the temperature above the threshold and the rate of development is assumed, just as a direct relation between gasoline per hour and miles per hour is assumed in figure 1. It will be noted that developmental units and degrees above the assumed threshold are of the same numerical value so that it makes no difference which is summed.

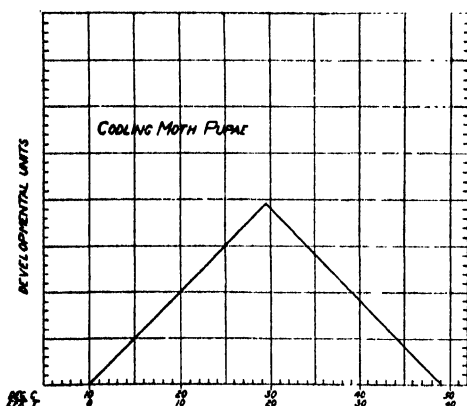


FIG. 3. SHOWING GLENN'S CURVE FOR THE DEVELOPMENT OF THE CODLING MOTH PUPA

The relations are the same as in figure 2 up to 29.5°C ., but above this point developmental units and degrees are not of the same numerical value. It is necessary to subtract twice the amount above 29.5 to make sum of developmental units and degrees the same.

of pupae during pupal life. This laid a basis for the idea of a constant. He further stated the *straight line limits* (see 15° to 30° , fig. 4) of a series of species. This means the temperature limits for rates of development within which the century old idea of summing temperatures holds.

The discrepancy between the summing idea and the actual velocities is not confined to the higher temperatures where the rate decreases rapidly, but at the lower temperatures development goes more rap-

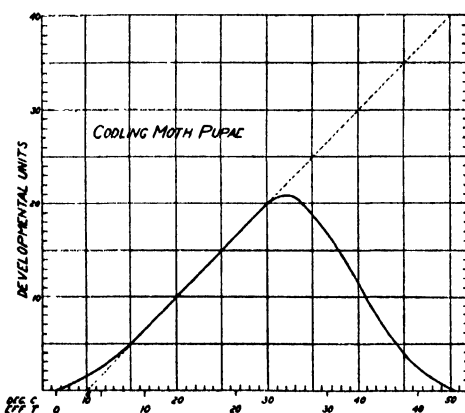


FIG. 4. SHOWING THE ACTUAL VELOCITY OF DEVELOPMENT CURVE FOR THE CODLING MOTH

Alpha is not the threshold. Between 6.5° and 16°C ., developmental units and degrees above the threshold are not of the same numerical value; the same is true above 30° , which renders sums of temperatures different from sums of velocities in developmental units. This makes the summing of temperatures a very inaccurate or impossible indicator of development.

idly than would be expected. Figure 4 shows the curve for the codling moth pupa for the average humidity. Glenn (curve shown in fig. 3) compensated for the low temperature deviation from the straight line by deducting too much at the higher temperature.

The use of inaccurate methods such as Glenn's, makes predictions uncertain in the years of exceptional conditions when pests are likely to make unusual progress.

This results in failure of remedial measures when success is most needed.

In the writer's study of the codling moth (1927), constant and variable temperature experiments were carried on so as to draw curves similar to figure 4.

Ludwig (1928) in *Physiological Zoology* (1:358-389) states that the writer's experiments "were conducted under varying conditions found in the field and were not verified by carefully controlled experiment," whereas a large series of experiments were run over the pupal life with variation of 0.6°C . and with humidity and evaporation known and controlled. He also refers to the writer's "thermal constants," etc., where these terms are erroneous and the *Developmental Total*, was actually used.

The vertical scale of figure 4 is velocity in developmental units (see below). Between 15° and 30°C . (medial temperatures) the velocity curve is a straight line which conforms to the law of the equilateral hyperbola. Within these limits the product of time and temperature (above 10°C .) is a constant. It will be noted that the straight line portion of the curve for the codling moth pupa with its extensions is identical with figure 2, in which 10°C . is the threshold.

THE DEVELOPMENTAL UNIT

The developmental unit is the difference between the amount of development taking place in one hour at any one degree of medial temperature, and that at a temperature one degree higher, for example, between 20° and 21°C . In figure 2, developmental units and *degrees* are of the *same numerical value* so that the result is the same when one sums temperature above α (10°) or developmental units above α on the vertical scale. This is due to the fact that the reciprocal of an equilateral hyperbola divides the angle between the axes of ordinates and abscissae in half and makes an angle of 45° with each of them (see fig. 1).

To further illustrate the meaning and value of the developmental unit, the 3600 developmental units are required to complete development. This is the product of time and temperature within the straight line limits. It is completed in 360 hours at 20° (10° above $\alpha = 10^{\circ}\text{C}$.) and 327.27 hours at 21° (11° above α) hence one degree increase in temperature reduces the time from 360 hours to 327.27 hours or 32.727 hours.

$$\begin{array}{r} 3600 \div 327.27 \text{ at } 11^{\circ} = 11 \text{ units per hour} \\ 3600 \div 360. \quad \text{at } 10^{\circ} = 10 \text{ units per hour} \\ \hline 1^{\circ} = 1 \text{ unit per hour} \end{array}$$

In many cases, e.g., in the case of plants and some animals at particular periods, developmental units have a definite meaning. Thus for temperature exposures of the Indian corn seedlings (for 12 hour periods) the centigrade degree-hour-unit has a value of 0.15 mm. elongation. This is determined between 18°C . and 28°C . but above or below this range 0.15 mm. is the unit regardless of other considerations. In the case of the tree cricket (Shull) a degree (C)-hour-unit is 459 chirps. It is determined between 17° and 22° , but at high and low temperatures, the unit is merely 459 chirps.

VELOCITY CHARTS FOR TEMPERATURE AND HUMIDITY

In the case of the codling moth a large series of experiments were run at different relative humidities so that a curve for temperature effects at several different humidities, e.g., 90 per cent, 80 per cent, 70 per cent, 60 per cent, 40 per cent, etc., could be drawn. If velocity curves applicable to these humidities are cut out from cardboard and stood upright on lines labeled in relative humidity on one axis and temperature on another the surface of a (fig. 5) ridge may be formed. Height above the base is then velocity of de-

velopment. By drawing lines on the surface of the solid connecting equal heights the contours shown on figure 6 are formed, and a chart showing velocity of development at any combination of temperature and humidity is thus made by projecting these onto a flat surface. The chart is based upon constant temperatures within the

sensations. Abbe, who in 1898 published an article on the curves of comfort, mentioned a chart similar in principle, which he had made but which he did not publish. Various others, especially engineers, followed with comfort charts. Pierce (1916) presented a schematic chart showing concentric ellipses corresponding to time to

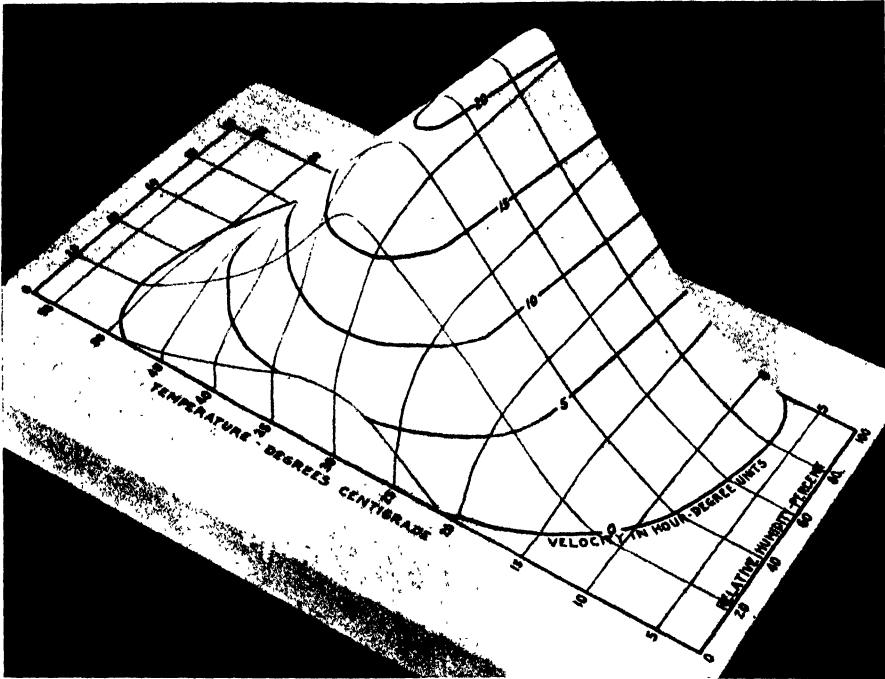


FIG. 5. SHOWING THE MODEL MADE FROM A SERIES OF VELOCITY CURVES LIKE FIG. 4, ONE FOR EACH DIFFERENT RELATIVE HUMIDITY

They were cut from paste board and fastened in position above the humidity to which they correspond and the space between them filled with plaster of Paris. The lines on the surface connect equal velocities and are contour lines running along the side and around the end of a ridge.

heavy line on figure 6, and upon variable temperatures outside of this. The central stippled areas indicate that portion of the temperature-humidity range within which the law of the equilateral hyperbola holds good.

This idea for a chart with three conditions in one plane probably originated, so far as weather and the responses of organisms is concerned, in the idea of comfort

complete stages, conditions for starting hibernation, etc., on a temperature-humidity chart.

The writer applied his codling moth chart (fig. 6) to work out the dates that could have been predicted had it been used in 1915, 1916, and 1917 to predict the time of emergence at Olney, where Glenn (1922) did his work. There were hundreds of pupae whose theoretical time for

emergence could be worked out and compared with the actual time. The agreement between the two was good to a noteworthy degree (Shelford, 1927). The deviation from average rates was made

establishing a standard time for the stages. Similar methods were applied in making a chart for the other stages of the life history, demonstrating that the law of summing temperatures holds for a limited range of temperature only, too small

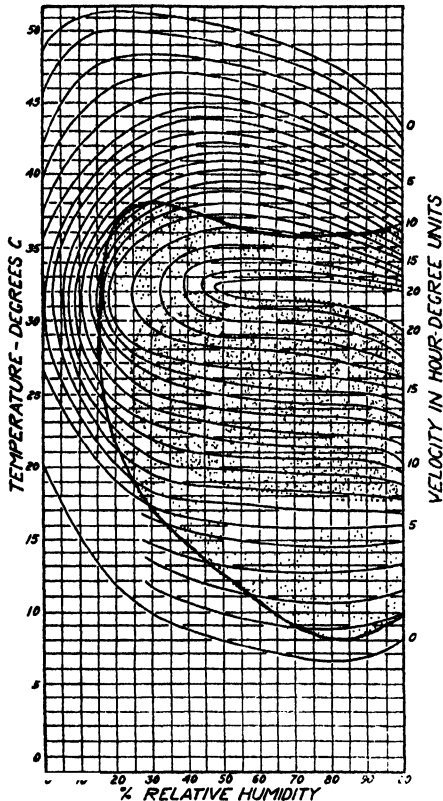


FIG. 6. SHOWING THE EQUAL VELOCITY CHART IN WHICH THE LINES ON THE MODEL IN FIG. 5 ARE PROJECTED ONTO A FLAT SURFACE

The lines connect combinations of temperature and moisture giving the same rate of development. A table was made showing the rates in developmental units by reading them off the chart for the various combinations of temperature and humidity. This was used in predicting times of appearance of moths.

clear, and it was found that rising temperatures lower development and falling temperatures accelerate it. (Shelford, 1929). Rainy autumns decrease mortality and make development more rapid the following season. Thus a new field of response is brought into recognition by

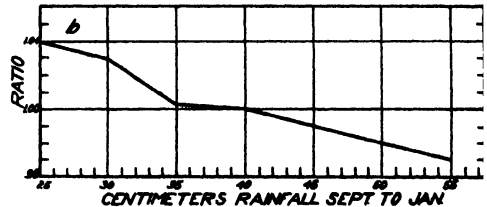
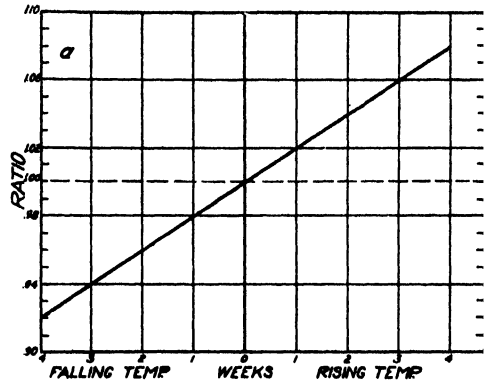


FIG. 7. SHOWING THE EFFECT OF RAINFALL (A) AND RISING AND FALLING TEMPERATURE (B) ON THE RATE OF DEVELOPMENT OF CODLING MOTH PUPAE

The evaluation of these and other factors was made possible by first evaluating temperature and moisture so that their effect was eliminated from consideration. (a) When temperature falls from day to day the length of the pupal life is progressively decreased; when it rises from day to day it is progressively increased. (b) Autumn and winter rainfall prepare the larvae for pupation favoring the breaking up of dormancy; perfection of this process appears to favor rapid development.

a range to permit its application to more than occasional days.

The general results show that the temperatures cannot be summed to indicate amount of development. This is best indicated in figure 4, where sum of temperature is contrasted with sum of develop-

mental units. It is not correct to refer to the sum of temperature for any process under ordinary weather conditions. This is the reason that degree-hour developmental units are necessary. The average number of these with uniform stock and food and for a long series of outdoor results constitutes the basis for standard time to complete a stage under any set of weather conditions. This in turn gives a value to individual variation which amounts to plus or minus 8 per cent for pupae and eggs and 16 per cent for the larvae.

This and other things are the general

fruits of studies started with observations "du thermomètre" made by Réaumur almost two hundred years ago. On the whole the net result in the way of practical application to agriculture, public health, etc., has been large; altogether larger than the contributions of those who have tried to relate the rates of development at different temperatures to chemical reactions, etc., and greater perhaps than the contributions to the same fields by plant physiologists who denounced phenology, and according to Oettingen offered no substitute.

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HISTORICAL SURVEY OF THE DEVELOPMENT OF THE SYMPATHETIC NERVOUS SYSTEM (*Concluded*)

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Histogenesis of the Autonomic Nervous System (Continued)

S. Uchida ('24) studied the development of the sympathetic nervous system in birds, in mammals and in reptiles. In 48 hour chick embryos there is no trace of sympathetic primordia. The ventral roots appear as growing fibers. The spinal ganglia are developing from the neural crest as cellular strands running in the mesenchyme on the lateral aspect of the spinal cord. During the third day, the spinal ganglia have given rise to a posterior root extending as far as the ventral root. The following day shows well developed spinal nerves. A very few cells are found migrating along the ventral roots and small cellular clusters are found near the dorsolateral angles of the aorta, without communicating rami. At the end of the fourth day, there exists a continuous sympathetic chain beginning at the level of the vagal ganglion. The vagus nerve can be followed to the superior part of the oesophagus. In embryos five days old, a periaortic sympathetic net has developed but no peripheral migration is to be found. Remak's nerve originates from the aortic plexus at the base of the mesentery. Sympathetic nerve cells are found in the adrenals, in the pancreas, in the intestinal wall and in the kidneys; they are in direct continuity with the primary sympathetic chain. At the end of the same day, branches and cells of the vagus nerve

form the perioesophageal plexus and the peribranchial plexus in exclusive connection with the vagus nerve and without any participation of the sympathetic trunks. A small nervous trunk originates from the sacral spinal nerves ventrally to the origin of the communicating rami, representing the first appearance of the nervus pelvici of the sacral autonomic system. From this nerve neuroblasts migrate ventrally to form the hypogastric plexus. The primary sympathetic chain disappears progressively and is very nearly gone at the end of the fifth day. During the sixth day, the secondary sympathetic chain appears. The vagus now extends all over the stomach to the pylorus and to the superior part of the small intestine. The vagus ganglion cells are very numerous in the gastric wall, become rare at the pyloric region and are practically absent in the small intestine. The mesenteric nerves reach the intestinal tract near its ileocaecal junction. During the seventh and the eighth days the sympathetic trunks send their fibers and cells into the various thoracic plexuses, which become vago-sympathetic plexuses. The abdominal plexus is still purely sympathetic and the vagus nerves reach it only later.

This description of Uchida is very interesting and represents in fact a sort of amendment to Kuntz's theory; it considers the origin of the pulmonary, cardiac, oesophageal, gastric, hepatic and pan-

creatic plexuses as vagal; the duodenal and intestinal plexuses are purely sympathetic. He refers to an experimental investigation of his but does not give any accurate description of it. The destruction of the dorsal half of the spinal cord by the electrolytic method on one side, provokes a unilateral absence of the spinal ganglia. The sympathetic ganglia are normally formed on both sides. The prevertebral and visceral plexuses are normal as well as Remak's nerve and the vagi. We might wonder what was the result expected by the author from this unilateral destruction, about the extension and the operating stage of which he does not give any details.

In mammals, his description does not bring in very original facts. He again shows the vagal origin of the pulmonary, cardiac, oesophageal and gastric plexuses while the kidneys, adrenals, intestine, pancreas and spleen are first innervated by the sympathetic system.

C. Smith ('24) studied the origin and development of the carotid body in very complete series of mammalian embryos. The carotid bodies are innervated by a pharyngeal branch of the glossopharyngeal nerve, by the pharyngeal branch of the vagus and by numerous twigs coming from the superior cervical sympathetic ganglion. In the rat the glossopharyngeal nerve shows embryonic sympathetic cells along its course. They seem to have a really glossopharyngeal origin and do not result from sympathetic anastomoses. The vagal branch does not show any embryonic sympathetic cells until the peripheral part of the body is reached; at this point numerous sympathetic cells are given off by the sympathetic branches. In calf embryos, besides the main contribution from the cervical sympathetic ganglion, a few cellular elements of the nervous supply of the carotid body are directly derived from the ninth and tenth cranial nerves.

In an extensive paper dealing mainly with the influence of the nervous system on the limbs of the Anura, Hamburger ('28) describes a few interesting points concerning their peripheral nervous system. After having removed one half of the spinal cord in six segments at the stage of closing neural folds, he finds a complete regeneration of the dorsal quarter of the cord. The motor half is never regenerated. These results corroborate the experiments of Hooker ('17-125) and of Braus ('05). The absence of regeneration found by Harrison, Kuntz, Müller and Ingvar is probably due to the fact that in these experiments the dorsal half of the cord was removed throughout its entire length. It must be remarked that the existence of a fully round neural tube does not necessarily mean regeneration. It may be a mere shifting of the material of the uninjured half or of the nearest segments. As far as the sympathetic system is concerned, no general idea could be drawn from his results. He considers that these corroborate the theory of the origin of the sympathetic chains from the spinal cord, although in a few cases he did not find the communicating rami. It is obvious that these cases represent the result of a cranio-caudal migration of the sympathetic elements from the nearest segment where a communicating ramus is found.

H. B. Adelmann ('25) studied very extensively the development of the cranial sympathetic ganglia in rat embryos. We shall consider only that of the vagus complex. This anlage is first seen in embryos of eight somites as a cellular mass interposed between the lateral edge of the neural plate and the ectoderm. At nine somites proliferation takes place and the cells migrate laterally and ventrally to come in contact with the ectoderm. Caudally the IX-X crest becomes somewhat more diffuse and is directly continuous with the spinal neural crest. Embryos of

24 somites are the first to show a definite vagal proliferation, though it is impossible to define the exact limits of it. Two cords of neural crest cells connect the glosso-pharyngeal and the vagal anlagen, while another strip of crest material extends caudally to join the spinal neural crest. The nodosal swelling appears at the stage of 31 somites. Some caudal extension has occurred, though, being very near the ectoderm, no direct contact can be observed between it and the vagal anlagen. The ganglion nodosum of the 34 somite embryo extends caudally over the territory of the fourth arch and bends ventrally behind the ultimobranchial body. A cellular extension of it can be traced to the root of the lung buds. The ganglion in a few sections is located close to the ectoderm without any noticeable fusion. In a 14 day embryo there is an intimate fusion between the root ganglia of the glosso-pharyngeal and vagus nerves. The inferior portion of the petrosal and the superior part of the nodosal ganglion are also intimately related. These connections are constant and primary, since the ninth and tenth anlagen are derived from an essentially continuous postotic proliferation of neural crest which is in direct prolongation of the spinal neural crest. There is thus no apparent contribution of any placode to the vagus ganglion; some adhesion can be found without migration of ectodermic elements.

R. A. Knouff ('27) studied very extensively the development of the cranial ganglia in the frog. His very careful and complete studies represent the most important piece of work carried out in this particular subject. We shall refer only to the development of the vagal complex. The vagal division of the neural crest grows from the dorsal border of the hindbrain downward and extends into the branchial region. When the second, third and fourth branchial pouches appear, the neu-

ral crest becomes subdivided so that each of these arches contains a small mass of cells from the non ganglionic portion of the vagal crest. This portion becomes constricted into two parts; the inferior contributes to the formation of two visceral ganglia (X and X_2). The neural crest cells of X_2 come in contact with an ectodermal thickening behind the fourth branchial pouch, which represents an epibranchial placode and probably gives a small contribution to the ganglion. The crest material X unites with two epibranchial placodes at the level of the second and third pharyngeal pouches. Above the constriction, the proximal part becomes the root connecting the vagus to the hindbrain and the distal portion differentiates into the jugularis ganglion (general cutaneous X). The dorsolateral and ventrolateral groups develop exclusively from the vagus lateral placode. The ramus intestinalis vagi is the medial projection of the visceralis X_2 . Knouff concludes that the visceral innervation supplied by the vagus nerve is almost exclusively furnished by the ventral part of the vagal crest, without eliminating a possible small contribution of the epibranchial placode.

In an outstanding series of experimental researches, Stone ('22) studied the development of the cranial nerves, in order to distinguish the rôle played by the placodes and by the neural crest in their constitution. As far as the vagus is concerned, he shows that the lateral line system is derived entirely from placodic material, while the neural crest contributes to the formation of the branchial cartilages and to the general visceral portion of the vagal ganglion. This last conclusion is supported by the fact that the removal of the corresponding neural crest cells leads to a definite rarification of the visceral fibers. This experimental work of Stone is confirmed by the recent publication of Knouff.

The rôle of the placodes and the neural

crest in the formation of the cranial ganglia seems to be clearly discriminated in amphibians. In the mammalian material, however, a considerable confusion does exist, and if we take the publications of DaCosta ('23), Bartelmez ('24), Adelman ('25) and a few others no actual theory could be drawn. The embryogenesis of the peripheral part of the autonomic nervous system has been entirely neglected in all these studies. Although the purely anatomical facts are very numerous, only a few data are known concerning the endings in the various organs and the immediate changes following the establishment of the nervous connections. In the pancreas of various mammals, the author ('25-'27) has shown that the primordia of the islets of Langerhans are very closely related to the ganglionic elements. The nervous supply of the endocrine system in the young stages of the development of the pancreas forms a well defined net, the islets being in intimate relationship with the ganglia and earning the denomination of "sympathetico-insular complexes." This pancreatic nervous network is directly continuous with the solar plexus, and the ganglionic cells are probably to be considered as true sympathetic elements. Numerous authors, for example Nelis ('26) and DeCastro ('25), tend to assume that these elements are parasympathetic in nature, and further studies are needed to discriminate the exact significance.

The rôle played by the vagus nerve in the visceral innervation has been studied very extensively from both anatomical and physiological standpoints. The anastomotic branches between the vagus and the sympathetic chain were frequently observed and analyzed. Ranson ('14), Molhant ('10), Iwama ('25), Chase ('16), Tokura ('25), Onodi ('84), Broman ('95), Edgeworth ('92), Michailow ('09), Dun-

can ('28), Uchida ('28) and others tried to elucidate their real nature by experimental methods. No agreement exists and further research is needed. The existence of these connecting branches does not allow any doubt, and they can perhaps explain many discordant results of physiological experimentation. The vagus nerve and the sympathetic cord might be considered as vago-sympathetic trunks, the excitation of any one of which has necessarily a complex result, making a definite discrimination of sympathetic or parasympathetic action difficult, if not entirely impossible. Besides this anatomical disposition, the visceral innervation is a difficult study on account of the variations in different groups. Bayliss and Starling ('99) have proved that the stimulation of the vagus nerve in mammals provokes a contraction of both longitudinal and circular muscles of the intestinal wall and that neither one of these contracts after excitation of the splanchnic nerves. Elliott ('04) has shown that in birds the stimulation of the splanchnic nerves is followed by a very well marked contraction of the entire duodenal region. Dixon ('02) states that in the frog the musculature of the whole stomach contracts either upon stimulation of the splanchnic nerve or after direct action of adrenalin.

It is thus impossible to generalize from the physiological results. The distinction of sympathetic and parasympathetic systems in each group requires a complete embryological and anatomical knowledge of the constitution of the nerve trunks called "vagus nerve" and "sympathetic chain." We believe the actual distinction of sympathetic, parasympathetic and local innervations to be erroneous, owing to ignorance of the real constitution of the visceral autonomic nervous system.

If we make a general survey of the literature in order to know the classical opinion

about the development of the sympathetic system, we get only a chaotic idea, even concerning the fundamental points of the question.

As far as the primary origin of the sympathetic elements is concerned; the oldest theory considered the spinal nerves as giving rise by proliferation to sympa-

portant part of the sympathetic system came from a local differentiation of mesodermic elements.

Numerous observers consider the neural crest and the spinal ganglia as the exclusive source of the sympathetic cells, while others give the main rôle to the neural tube by means of migration along the motor

TABLE I
Primary Origin of the Sympathetic System

FROM SPINAL NERVES	SPINAL GANGLIA AND NEURAL CREST	SPINAL GANGLIA AND TUBE	MESENCHYME
BALFOUR, fishes MARSHALL, chick	ABEL, chick ALLEN, fishes	CAJAL, chick CARPENTER and MAIN, pig	BRUNI, chick, rat CAMUS, frog
NEUMAYER, <i>Lacerta</i>	HELD, series of vertebrates	FRORIEP, <i>Torpedo</i> , rabbit	DART and SHELLSHEAR, man
VANWIJHE, <i>Pristiurus</i>	HIS, man HIS, JR., chick HIS, JR., and ROMBERG, series of vertebrates HOVEN, chick MARCUS, <i>Torpedo</i> MAZZARELLI, birds MÜLLER, selachians MÜLLER and INGVAR, chick, frog ONODI, series of vertebrates RABL, <i>Pristiurus</i> SCHENK and BIRDSALL, chick, man STREETER, man	GANFINI, series of vertebrates GOORMACHTIGH, birds HOFFMAN, selachians, urodeles KOHN, mammals KUNTZ, series of vertebrates RAU and JOHNSON, sparrow UCHIDA, series of vertebrates	FUSARI, chick and mammals GOETTE, chick PATTERSON, chick REMAK, chick SCHULTZE, <i>Vespertilio</i> TELLO, series of vertebrates WEBER, man

thetic cells; this viewpoint has been entirely discarded during the last twenty years and has only an historical interest.

The theory of the mesenchymal origin of the sympathetic elements was inaugurated by Remak and found only a limited number of advocates. Recently it has received a real support in the publications of Tello, who attempted to show that an im-

ports. Both theories are supported by experimental studies, the results of which are diametrically opposite. These experimental researches agree in denying the mesodermal origin of the sympathetic cells. Table I summarizes these different conclusions concerning the primary origin of the sympathetic elements. It is impossible to disregard any one of the last three

mentioned theories and any embryological investigation carried out in this field should answer the following questions:

1. Do the sympathetic chains arise from the ectoblast or from the mesenchyme?
2. Along what spinal root is there a migration of sympathetic elements?

If we take into special consideration the visceral innervation, we also find a great deal of confusion, especially concerning the nervous supply of the small intestine.

4. What has the vagus nerve to do in the constitution of the visceral plexuses?

These four questions require a special answer for each group of vertebrates, and as far as possible need an experimental verification. The main features of the development of the autonomic nervous system will very probably be found identical in the entire vertebrate series; to them will it be possible to apply a general theory of embryogenesis and the variations found

TABLE 2
Primary origin of the innervation of the small intestine

MESODERM	VAGUS NERVE	SYMPATHETIC SYSTEM
CAMUS, frog DART and SHELLSHEAR, man FUSARI, chick, mammals ONODI, series of vertebrates REMAK, chick O. SCHULTZE, chiroptera TELLO, chick, mouse	ABEL, chick KUNTZ, series of vertebrates E. MÜLLER, selachians, chick STEWART, rat	BALFOUR, selachians DOGIEL, series of vertebrates FRORIEP, <i>Torpedo</i> , rabbit GANFINI, series of vertebrates HELD, series of vertebrates W. HIS, man W. HIS, JR., and ROMBERG, series of vertebrates KOHN, rabbit MEIKELJOHN, chick NEUMAYER, <i>Pristiurus</i> RAU and JOHNSON, sparrow SHENK and BIRDSALL, chick STREETER, man UCHIDA, series of vertebrates

Table 2 summarizes the main observations on this question. A mesodermal origin has been asserted by many observers, and Tello has recently given important confirmatory evidence. The primary sympathetic innervation is supported by many while the importance of the vagus nerve has been emphasized by a few noted investigators. Two other questions arise concerning this aspect of the problem:

3. Are some visceral ganglia derived from the mesenchyme?

in each particular group will enable us to understand the divergent physiological results in the light of anatomical and embryological facts.

Histogenesis of the chromaffin part of the adrenals

A complete review of the literature concerning the development of the adrenals can be found in Poll's monograph; here we shall give briefly the main conclusion of the different investigators. In this field also there has been a great deal of confu-

sion; but the actual opinion concerning the primary origin of the chromaffin elements of the adrenals seems very generally accepted.

Leydig ('53), studying the suprarenals and interrenals in fishes, concluded that the suprarenals are embryological derivatives of the sympathetic system. Remak ('57) derived the chromaffin system from the sympathetic elements. He was considering the mesodermal origin of the sympathetic system and thus the primary mesodermal origin of the chromaffin elements. Balfour ('81) in elasmobranchs stated that the interrenal organs are of mesodermal origin, while the suprarenals are derived from the sympathetic ganglia located along the abdominal aorta. He was corroborated a few years later by Mitsukuri.

Gottschau ('83) in mammalian embryos noticed the intimate association of the chromaffin tissue with the cortical part of the adrenal and concluded that both are derived from the mesoderm. The same year, Janosik studying the same material observed cells of the peritoneal epithelium migrating into the mesenchyme in the region of the adrenals and stated that cortical and chromaffin components are both derived from the germinal epithelium. In mammals, Gray ('52), Valenti ('89), and Roud ('03) considered the medullary part of the adrenals to be mesodermal in origin. Minot ('94) in the human embryo found no evidence of the sympathetic origin of any part of the adrenals and supported the theory of their mesodermal origin. In reptiles von Mihalcovicz ('85) admits their common origin from the germinal epithelium. For Brauer ('00) the cortical part develops from the mesenchyme, for Weldon ('85) and Hoffmann ('00) from the pronephric epithelium, for Soulie ('03) from the peritoneal epithelium. All of them consider the chromaffin part of

the adrenals as originating from anlagen of the prevertebral sympathetic plexuses. In selachians, Haller ('01) considered that the chromaffin elements of the adrenals were related to the mesonephric tubules. In the same group Semper ('75) tried to show their origin from the mesenchymal cells. Those observations were disproven by Balfour ('78) in *Scyllium* and by Hoffmann ('02), who very clearly showed the sympathetic origin of the chromaffin elements. V. Brunn ('72), Sedgwick ('80), Valenti ('93) and Minervini ('04), studying chick embryos, described the mesodermal origin of the chromaffin part of the adrenals. Schultze ('97) in *Vespertilio* described the entire adrenal anlage as originating from the sympathetic ganglia, showing only later a differentiation into cortical and medullary parts.

Fusari ('93) studied the development of the adrenals in chick and in mammals. In a 78 hour chick embryo he describes cellular bands extending from the sympathetic chains toward the region between the aorta and the cardinal veins. At 90 hours the sympathetic chains are well marked on both sides of the prevertebral region; they send numerous cellular strands toward the epithelial bands differentiated from the peritoneal epithelium. From that moment on, and still more clearly at the stage of 96 hours, the anlagen of the adrenals show their double origin, from the peritoneal epithelium and from the prevertebral sympathetic plexuses. According to Fusari, the sympathetic plexuses arise by differentiation of the mesoderm.

Soulie ('03) was unable to corroborate the descriptions of Fusari. In the 162 hour chick embryo a big ganglionic mass is located near the dorsal aspect of the interrenal anlagen at its distal end. At this moment the first distinction is to be seen between the sympathoblasts and the phео-

chromoblasts. The topographical relations remain such to the ninth day of incubation and the penetration of the latter elements into the interrenal substance occurs only around the tenth day. Flint ('00) in pig embryos showed that the cortical develops first, the medullary appearing later as a grouping of cells wandering in from the outside. He required further proof before admitting the sympathetic origin of these migrating elements. Aichel ('00) says that in selachians the interrenals alone are homologous to the adrenals of higher vertebrates and that they arise from the peritoneal invaginations of the prenephros; the so-called suprarenals would be derived from retrograding canals of the latter organ. In mammals both parts of the adrenals are derived from the epithelium of the pronephric tubules. Wiesel ('01), though studying too far developed pig embryos, observed that the cortical part is derived from the peritoneal epithelium, the chromaffin medullary part from the prevertebral sympathetic plexuses.

H. Rabl ('91) in birds considers the chromaffin cords of the adrenals as originating from the penetration into the interrenal anlagen of the elements of a large ganglion closely related to it. This ganglion is the result of a migration of numerous indifferent cells from the prevertebral sympathetic ganglia. Soulie ('03) studied the histogenesis of the adrenals in various reptiles. In a 10 mm. long embryo of *Lacerta* the first lumbar ganglia send out a few cellular bands which become connected with one another and form a big cell-mass located dorsally to the anlagen of the interrenal system. A certain amount of connective tissue between the two anlagen establishes a clear distinction. The chromaffin part of the adrenals originates directly from the lumbar sympathetic ganglia.

Brauer ('03) described at length the development of the adrenals in *Hypogeophis*. Cellular groups become detached from the sympathetic ganglia. The cells are very clearly distinguished by their size, their granular cytoplasm and their avidity for stains. These cells migrate along the lateral and ventral aspects of the aorta, and come in intimate connection with the interrenal system.

Kohn ('03) studied very extensively the development of the chromaffin part of the adrenals in various mammals. In a human embryo, 19.5 mm. long, he describes numerous cellular groups extending from the sympathetic ganglia toward the region of the aorta. The differentiation of these elements begins in the ganglia, from which they migrate as cellular strands. At this stage, they are found only in the region of the adrenals, although a few chromaffin heaps may exist independent of the interrenal anlagen. In a 27 mm. embryo, the migration of the prechromaffin elements is found in the entire length of the sympathetic chains.

Bruni ('12) describes the first appearance of chromaffin cells in *Rana esculenta* at the stage of 27 mm. near the renal vein, in intimate contact with the lymphoid tissue of the mesonephros and the interrenal cord. He is unable to see any chromaffin heaps in the cephalic and cervical regions. Zuckerkandl ('12) presents a complete review of the literature concerning the chromaffin tissue. In a 19 mm. human embryo he verifies the description given by Kohn in a pig embryo 44 mm. in length. The chromaffin elements of the intercarotid gland are derived from cells situated in the nerves coming from the upper cervical sympathetic ganglion and forming the plexus intercaroticus. In the ganglia of the abdominal plexuses, the differentiation of chromaffin bodies begins at a time when the sympathetic cells have not yet

diverged from the original sympathochromaffin type (= sympathogeny). The statement of Soulie ('03) that the chromaffin cells do not develop until neuroblasts are present in the sympathetic ganglia can only be accepted as referring to the medulla of the adrenals, which is remarkably late in its differentiation.

Kuntz ('12) described extensively the development of the adrenals in the turtle. During the eleventh day of incubation, sympathetic cells migrate along the lateral surfaces of the aorta and may be observed in very close contact with the anlagen of the cortical substance. Later on, the prevertebral sympathetic plexuses develop and numerous cell groups may be traced from them toward the dorsal and mesial surfaces of the adrenals. A few cells are found among the cortical cells. These facts show very clearly the origin of the chromaffin part of the adrenals from sympathetic elements, which are identical with the "indifferent cells" found in the prevertebral plexuses. The chromaffinity appears only after a considerable interval of time of association with the cortical substance. It is, therefore, probable that the differentiation of those cells into chromaffin elements is stimulated by the influence of hormones produced by the cortical cells.

A. Jona ('13) studied the development of the interrenal and chromaffin tissue in the anuran amphibia. That question had been already studied by Srdinko, who described the first appearance of the interrenal system at 9 mm., by Soulie at 32 mm. and by Albrand at 29 mm. Soulie ('03) does not believe in the existence of chromaffin cells in the adrenals of the Anura in spite of the very clear observations of Giacomini ('02), Stilling ('98) and Grynfelt ('04.) At 5 mm. the interrenal organs appear as a massive proliferation at

the base of the mesentery. This cellular mass increases gradually in size and progressively detaches itself from the peritoneal epithelium, lying thus at the origin of the coeliac mesenteric vessels. Using the determination of partial length, i.e., from the apex of the head to the anal opening, she describes at 1 mm. isolated cells definitely different from the mesenchymal cells and showing the cytological characters of sympathogonies. It is only at 4 or 5 mm. that these cells differentiate either into phaeochromoblasts or into sympathoblasts. The chromaffin reaction is found in embryos of 3 to 12 mm. in partial length.

Hays ('14) studied the development of the adrenals in the chick. In a five day embryo, large, deeply stained cells are seen migrating ventrally from the prevertebral sympathetic plexuses, passing between the aorta and the groups of cortical cells. At 130 hours of incubation, a few of these sympathetic elements are penetrating into the cortical anlagen and become scattered throughout its substance. The first cellular differentiation is found in seven day embryos. The cells become smaller, their shape irregular, and they show a marked avidity for stains with a tendency to arrange themselves in cords. These cords break down, and during the ninth day most of the cells are found in small groups arranged around the venous blood vessels. From that moment on, no changes are found in the disposition of the two substances. The chromaffin part of the adrenals is derived from indifferent cells, which wander in from the anlagen of the prevertebral sympathetic system.

In dealing with the literature of the sympathetic system, we have already referred to the publications of Whitehead ('03), Rau and Johnson ('23), Goormaghtigh ('24) and Da Costa ('17). Their ob-

servations show conclusively that the chromaffin elements are derived from the sympathetic anlagen.

Actually it may be considered proved that the medullary part of the adrenals arises from sympathetic elements migrating toward the mesodermal primordium of the cortical substance. Table 3 summarizes the main opinions, and it will be seen

just as well differentiated as one developed from a graft taken from a nine day embryo. These results show conclusively that cells from the secondary sympathetic ganglia are not essential to the formation of the medullary cord in the chick adrenals. The sympathetic cells found at four days close to the cortical anlage represent the real primordium of the medullary system.

TABLE 3
Origin of the Chromaffin Part of the Adrenal

MESODERMAL TISSUES	SYMPATHETIC SYSTEM
AICHEL, selachians, moles	BALFOUR, selachians
BRUNI, frog	BRAUER, <i>Hypogeophis</i>
V. BRUNN, chick, dog	BRAUN, reptiles
CAMUS, frog	DA COSTA, chiroptera
GOTTSCHAU, mammals	DE WINNIWARTER, mammals
GRAY, chick	FUSARI, chick
HALLER, selachians	GOORMACHTIGH, chick
JANOSIK, chick, man, cat	HOFFMANN, series of vertebrates
V. MIHALCOVICZ, reptiles	JONA, frog
MINERVINI, chick, dog	KOHN, man, rabbit, cat
RATHKE, crocodile	KUNTZ, turtle
ROUD, mouse	LEYDIG, fishes, reptiles
SEDGWICK, chick	MINOT, man
SEMPER, selachians	MITSUKURI, rabbit
VALENTI, chick	POLL, series of vertebrates
	REMAK, chick
	O. SCHULTZE, chiroptera
	SOULIE, series of vertebrates
	SRDINKO, anurans
	WHITEHEAD, pig
	WIESEL, pig, man
	VAN WIJHE, selachians
	ZUCKERKANDL, man

that the theory of the mesodermal origin of the chromaffin part of the adrenals is no longer advocated.

A very interesting attempt has been made recently by B. H. Willier ('28) in chick embryos, to determine experimentally the origin of the chromaffin elements in the adrenals. By the method of chorio-allantoic grafts Willier shows that the adrenal formed from a four day implant is

He then questions the significance of the contribution from the secondary chain. This method of approach is a very promising one and it may give the answer to many important questions of embryogenesis of the adrenals and of the autonomic system.

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NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of THE QUARTERLY REVIEW OF BIOLOGY, 1901 East Madison Street, Baltimore, Maryland, U. S. A.

BRIEF NOTICES

EVOLUTION

THE ASCENT OF HUMANITY. *An Essay on the Evolution of Civilization from Group Consciousness Through Individuality to Super-Consciousness.*

By Gerald Heard. Harcourt, Brace and Co.
\$3.00 5 $\frac{5}{8}$ x 8 $\frac{1}{2}$; xiv + 332 New York

The author conceives the ascent of humanity to be a progress based on the evolution of psychical factors, leading from group consciousness through consciousness of the individual to a super-consciousness. He argues that in the most primitive forms of society all individuals were submerged in undifferentiated groups, societies which in many respects were analogous to communities of bees and ants. In the course of time, a consciousness of individuality emerged, at different times in different groups and under varying conditions, the earliest types being exemplified in the priest, doctor and king. In the present era, the scientific age, a higher form of consciousness is growing out of individualism, which seeks "not to acquire but to understand by a coöperative method." Just where this new form of consciousness will lead humanity is doubtful. How successful will it be in wrestling with the "con-

sciousness of individualism," which is still bursting forth with increasing vigor?

The author's concept is well worth considering in that he gives us a comprehensive survey of the progress of humanity from quite a new angle and raises numerous interesting problems. Many will disagree with his concept of superconsciousness and will lose interest in the latter part of the book where he leads the reader into a discussion of the value of psychic research.



MODERN MATERIALISM AND EMERGENT EVOLUTION.

By William McDougall.

D. Van Nostrand Co., Inc.
\$2.75 5 $\frac{1}{2}$ x 8 $\frac{1}{2}$; x + 249 New York

The author contributes this volume as a supplement to his *Body and Mind* recently noted in these columns. The contents were delivered as a series of lectures before the Louisville Presbyterian Seminary. McDougall continues to be one of the doughtiest examples of the class of humans referred to by De Morgan as paradoxers "individuals who hold views apart from the general opinion in subject matter, method or conclusion." He is an in-

trepid defender of a whole gamut of paradoxes running from Nordic Superiority to Psychical Research. In this work he espouses "teleological causation" as against the belief that "conscious thinking cannot affect the course of physical events." He rejects not only atomic materialism and its philosophic antagonist, vitalism, but what may be fairly said to lie between the position of these two, emergent evolution. What he has to say in criticism of the last has some novelty and weight. The evidence for his own contention, however, that Mind can control the future history of matter, which includes survival of personality after death, and inheritance of acquired characteristics, is as dubious as the thesis he defends.

An appendix of technical notes makes up half of the book and there is an index.



PREHISTORIC MAN IN GENESIS. *A Study in Biblical Anthropology Giving the True Reading of the First Chapters of the Bible and a Naturalistic Interpretation of the Tradition about Adam and Eve.*

By Rev. F. deP. Castells. Rider and Co.
5 shillings net London

4 $\frac{3}{4}$ x 7 $\frac{1}{4}$; 160

The author believes he has discovered historical facts back of the story of Adam and Eve. Adam was not the first created man, the *adam* were a group of Hindu Vaisyas whom the Elohim colonized among the aborigines of Eden. Eve was procreated in the customary way; the rib is a corruption of the text. Having broken a *tabu* by eating the fruit of the sacred trees, the settlers were exiled from Eden. We imagine that the Rev. F. deP. Castells, like some other reconcilers, will fall between two stools; his interpretation is not likely to commend itself either to the orthodox or to anthropologists.

GENETICS

VARIATION AND CORRELATION IN THE APPENDAGES OF THE HONEY BEE. *Memoir 121.*

By E. F. Phillips. Cornell University
Free, but edition limited Ithaca

6 $\frac{1}{4}$ x 9; 52 (paper)

Some of the conclusions which the author gives are as follows:

For the material studied, it appears that drones are considerably more variable than are working bees. The irregularity in cell size has a direct effect on variability by bringing about a lesser degree of homogeneity in the material, from which it may be concluded that the size of the cell directly affects the sizes of various parts of the body. This effect doubtless arises from the amount of food taken, although there may be some influence from pressure of the cell walls themselves, a suggestion which cannot be proved from the present material. The hooks on the hind wings are erratic in variability.

Abnormalities in venation give additional and conclusive evidence of the greater variability of the drones, which arise from unfertilized eggs.

There is a high correlation in the plane of bilateral symmetry, less in homologous and analogous parts of consecutive segments, and still less between parts of appendages lying in a dorsoventral plane.



THE GENETICS OF THE TETTIGIDAE (Grouse Locusts.) (*Contribution No. 105, Department of Zoology, Kansas State Agricultural College and Agricultural Experiment Station, U. S. A.*)

By Robert K. Nabours. Martinus Nijhoff
4.40 guilders The Hague

6 $\frac{3}{8}$ x 9 $\frac{3}{8}$; 78 (paper)

In this paper are reviewed, aside from the biology and breeding habits of the Tettigidae, the author's genetic work in the family. His experiments have dealt with some of the dominant color patterns, and the normal recessives of the following species: *Paratettix texanus*, *Apotettix eurycephalus*, *Tettigidea parvipennis pennata* and

Telmatettix arcticus. The author gives many tables pertaining to these experiments and a number of plates showing color patterns. He includes a lengthy list of references and an index.



THE CHILD'S HEREDITY.

By Paul Popenoe.

The Williams and Wilkins Co.,
\$2.00 $5\frac{1}{2} \times 8\frac{1}{2}$; xiii + 316 *Baltimore*

A popular handbook of human inheritance. There is a bibliography and an index.



GENERAL BIOLOGY

THE GREAT APES. *A Study of Anthropoid Life.*

By Robert M. Yerkes and Ada W. Yerkes.

Yale University Press
\$10.00 *New Haven*

$7 \times 10\frac{1}{2}$; xix + 652

This stately and splendidly printed volume is a monument to the industry and the critical judgment of the authors. It will stand for a long time as the basic work of reference for anyone interested in the biology of the primates. The literature has been thoroughly combed from classical times to the present, and brought into correlation with modern experimental work in the field, of which the senior author is the acknowledged and esteemed leader. The book is divided into six parts, of which the first is historical, and the last comparative and summarizing. The other four deal successively with the gibbon, the orang-outan, the chimpanzee, and the gorilla. It is extensively illustrated, thoroughly documented (the bibliography covers 25 double column pages), and meticulously indexed. The tone throughout is a combination of rigorous

critical scepticism, accompanied with enthusiastic presentation of problems urgently awaiting study. The book is a permanently valuable contribution to the literature of biology, which does honor to its authors, and to American biology.



THE SCIENCE AND PHILOSOPHY OF THE ORGANISM.

By Hans Driesch.

The Macmillan Co.
\$6.50 $5\frac{1}{2} \times 8\frac{1}{2}$; xii + 344 *New York*

In this second edition, the famous exponent of vitalism summarizes in a single volume, the views originally elaborated in the Gifford Lectures of 1907 and 1908. Since that time almost every work devoted to the basic principles of biology has had something critical to say of Driesch's *entelechy*, but he continues to have a provocative effect on biologic thinking. A re-reading does not modify our original impression that *entelechy* is essentially a metaphysical word for scientific ignorance. The physical explanation is applied to progressively more fundamental biological phenomena, and where it seems to finally break down, *entelechy* is called in. So far as it represents simply this negative aspect of thought, vitalism does not fall within the domain of science at all, since it appears always at the moving point where science leaves off. In this respect, it is distinctly less satisfactory as a philosophy of nature than the more recently elaborated organic philosophies popularly best known as *emergent evolution*. These latter attempt to comprehend certain positive aspects of natural phenomena not adequately represented in a strictly mechanistic idealogy. In his new preface, the author promises that this edition is brought up to date, but no consideration at all is given to the numerous criticisms that have been made of his views, nor to

rival philosophic systems that have been developed to meet the problems with which he deals. There is an index.



ZELLTEILUNG UND STRAHLUNG.

By T. Reiter and D. Gabor.

Julius Springer

18 marks 8 x 11; 183 Berlin

This is the most extensive independent research which has been made to test the correctness of Gurwitsch's work on "mitogenetic rays." The authors confirm the existence of an action at a distance of certain living objects upon the growth region of onion root tips and assert that this action is a radiation phenomenon in the physical sense. The book contains a great mass of detailed physical and biological observations.



DIE PHILOSOPHIE DES ORGANISCHEN BEI SAMUEL BUTLER.

By Rudolf Stoff.

Phaidon Verlag

5 marks 4½ x 7½; 109 Wien

An account for the German reader of Butler's biological writings. His views on inheritance as a form of memory and on the personal identity of parent and offspring are adequately presented, but much of the flavor of Butler's personality is necessarily lost in a résumé.



MEAT THROUGH THE MICROSCOPE.

Applications of Chemistry and the Biological Sciences to Some Problems in the Meat Packing Industry.

By C. Robert Moulton.

University of Chicago Press

\$5.00 5½ x 8½; xii + 528 Chicago

In this book are discussed the problems of the meat packing industry and the

application of chemistry, bacteriology and other biological sciences to these problems. There is much valuable information given, in non-technical language, concerning the many phases of the industry from the keeping and curing of meats, the health of the animals, etc., to the value of the numerous by-products of the industry.



ECONOMIC BIOLOGY. A Text for Students of Agriculture and General Biology.

By George P. Weldon.

McGraw-Hill Book Co., Inc.

\$2.50 5½ x 8; xi + 457 New York

A text book of high-school grade emphasizing facts of practical and economic importance.



DIE BINNENGEWÄSSER. Einzeldarstellungen aus der Limnologie und ihren Nachbargebieten. Band VII: Die Biologie der Moore.

By O. Harnisch.

E. Schweizerbart'sche Verlagsbuchhandlung
16 marks (paper) Stuttgart

17.50 marks (bound)

6¾ x 10; 146

DIE BINNENGEWÄSSER. Einzeldarstellungen aus der Limnologie und ihren Nachbargebieten. Band VIII: Der Hochgebirgssee der Alpen.

By Otto Pesta.

E. Schweizerbart'sche Verlagsbuchhandlung
17.50 marks (paper) Stuttgart

19 marks (bound)

6¾ x 10; xi + 156



HUMAN BIOLOGY.

GREENLAND. Vol. II. *The Past and Present Population of Greenland.* By The

Commission for the Direction of the Geological and Geographical Investigations in Greenland.

Oxford University Press

\$14.00 (U. S. A.) New York and London
35 shillings net (C. A. Reitzel, Copenhagen)

7 x 11; 415

In this second volume on Greenland, published by the Danish Commission for investigations in Greenland, there appear the following papers: The Greenlanders of the Present Day, by Kai Birket-Smith; Intellectual Culture of the Greenlanders, by G. W. Schultz-Lorentzen; Eskimo Archaeology, by Thomas Thomsen; On the Icelandic Colonization of Greenland, by Finnur Jonsson; Old Norse Farms, by Daniel Bruun; The Finds from Herjólfssnes, by P. Nörlund.

The first paper, which is by far the longest in the group, includes not only a detailed study of present day customs, habitations, furnishings and household implements, but much concerning the influence of previous immigrations on the physical characteristics and customs of the natives. It is the author's experience that individuals of mixed blood are "superior to the unmixed Eskimos by a greater susceptibility and power of adaptation as well as by greater energy and a wider outlook in economic matters." The Polar Eskimos he believes to be more cleanly than most other Greenlanders, and the Polar Eskimos are the most northerly people of the earth. But, the author points out, poverty and lack of cleanliness go hand-in-hand, in Greenland as in more civilized countries, and these northern-most people are, in a sense, well-to-do, being a small tribe with vast hunting grounds at their disposal. Matches are now widely used by all Eskimos, the old fire-making tools fast falling into disuse. Tea is the favorite beverage of the Polar Eskimos who ac-

quired the habit through their contact with the Anglo-Saxons, while the west coast Greenlanders hold fairly firmly to their habit of coffee drinking, which they acquired from another group of peoples.

The intellectual culture of the Greenlanders has, of course, been very greatly influenced by their contact with foreigners. This influence is especially noticeable in the linguistic field. The three factors which are the main sources of the complex ideas of the Greenlanders are observation, tradition and a vivid, impressionable imagination. With hundreds of years of battling with unusual conditions as an ancestral background, the Eskimo, within his limits, is a unique individual. He can find his way where no marks are visible. He estimates time with marvelous accuracy, not only when the sun is visible, but when it is not, by the changes of the tide. His knowledge of the lives of the animals with which he is in any way concerned is complete. He is thoroughly familiar with their habits and every detail of their anatomy.

The last four papers in the volume present many interesting and important facts concerning the ancient inhabitants of Greenland. Of especial interest is the account of the discoveries at Herjólfssnes, where evidence points to a Norse settlement at about the year 1200.



LIFE AND WORK IN PREHISTORIC TIMES.

By G. Renard.

Alfred A. Knopf, Inc.

\$4.50 6 x 9½; viii + 228 New York

Speculation concerning the life and work of peoples who lived thousands of centuries ago based on a few scattering remains must at best be only an approximation to the facts as they actually

existed. This book undoubtedly furnishes material for much discussion and dissension among anthropologists. The lay reader will generally accept it as an interesting and stimulating account of ancient man's activities. The writer deals with the very earliest periods of prehistory, that is, from the origins of mankind up to that period when most civilized races commenced to record ideas in writing. His method is synthetic, considering in turn "the various activities by which man has sought to satisfy his needs and show how each was carried on until the time when it enters history not without projecting into our own times not a few curious survivals."

The book contains a number of interesting illustrating reference lists, and an index. It is one of the volumes in the "History of Civilization" series, edited by C. K. Ogden.



FROM THE PHYSICAL TO THE SOCIAL SCIENCES. *Introduction to a Study of Economic and Ethical Theory.*

By Jacques Rueff (Translated by Herman Green, with an Introduction by Herman Oliphant and Abram Hewitt).

The Johns Hopkins Press

\$2.00

Baltimore

5½ x 8½; xxxiv + 159

The burden of M. Rueff's song is that the physical and the social sciences are alike in their essential methodology. In mechanics the concepts of mass and force and the laws of motion are created by us so that we may deduce from them the observed behavior of moving bodies. Similarly in the different systems of ethics we create God, or the categorical imperative, or the hedonistic principle, in order that we may deduce from them the right-

ness or wrongness of particular classes of acts which we have observed empirically to be judged right or wrong by the society in which we live. Ethical or legal or economic theories have no absolute or *a priori* validity, but are of value only insofar as we can deduce from them the observed facts of ethics or law or economic activity. We advise the social scientists to read, mark, learn and inwardly digest this little book. It will certainly save them from much vain disputation and may aid them in bringing order out of the confusion of observed social phenomena.



MARRIAGE AND DIVORCE 1927.

Statistics of Marriages, Divorces, and Annulments of Marriage. Sixth Annual Report.

Department of Commerce Bureau of the Census

U. S. Government Printing Office

15 cents

Washington

5½ x 9½; 90 (paper)

This report presents the results of the ninth Federal investigation of marriage and divorce in the United States. The first covered the twenty-year period 1867-1886, the second 1887-1906, the third, which was to continue these to 1916, because of intervening war conditions is limited to 1916. From 1916 till 1922 reports are omitted, but beginning in the latter year they have been issued annually. The main contents are categorized under the headings Marriage Statistics, Divorce Statistics, Annulment Statistics. There are tabular and graphic analyses of the secular trends of the marriage and divorce rates, and detailed tables classifying divorces by cause, party to whom granted, duration of marriage, children affected, etc. The material included is intelligently and succinctly reviewed in the summary discussions.

DANGER SPOTS IN WORLD POPULATION.

By Warren S. Thompson.

Alfred A. Knopf, Inc.

\$3.50 5½ x 8; xxi + 343 New York

A survey of the trends in population growth of the various nations and of the resources available to each nation to support its future increments of population. Dr. Thompson concludes that the Japanese, with a rapidly increasing population and meagre natural resources, are not likely to permit the British and the Dutch to play dog-in-the-manger much longer in Borneo and New Guinea. Nor are the Italians likely to be content with a situation in which they are kept in on every side. The remedy which he suggests is a voluntary redistribution of land and resources among the peoples of the world in proportion to their needs, a remedy which, however distasteful it may be to the nations losing territory by the process, would at least be less disastrous for them than an involuntary redistribution following another World War. This, however, will not be a permanent solution of the population problem, but will merely tide over the transition period until the practice of birth control can be adopted by the various nations.

This is an important book, which will well repay reading. However, we very much doubt whether Dr. Thompson will convince the governments of Great Britain and France of the wisdom of the policy he recommends.



THE MAKERS OF CIVILIZATION IN RACE AND HISTORY. *Showing the Rise of the Aryans or Sumerians, Their Origination and Propagation of Civilization. Their Extension of it to Egypt and Crete, Personalities and Achievements of Their Kings, Historical*

Originals of Mythic Gods and Heroes with Dates from the Rise of Civilization about 3380 B.C. Reconstructed from Babylonian, Egyptian, Hittite, Indian and Gothic Sources.

By L. A. Waddell.

Luzac and Co.

28 shillings

London

5¾ x 9¼; lvi + 646

According to Colonel Waddell, ancient inscriptions, interpreted in the light of the Hindu *Purāṇas*, reveal the true origin of civilization. The Sumerians, it seems, were an Aryan race who developed the original civilization of Mesopotamia and extended it to Egypt, Crete, Indo-Persia, and Ancient Europe. Their early kings were the originals of the gods and heroes of classic antiquity as well as of the Eddas and the Arthurian cycle. The Holy Grail found its resting place, not at Montsalvat, but at Nippur in Mesopotamia. Plainly Colonel Waddell has an Aryan bee in his bonnet, and the temptation is to dismiss him as another paradoxer. However, he knows his subject more thoroughly than most paradoxers; we shall, therefore imitate the admirable circumspection of Professor Sayce, in reviewing one of Colonel Waddell's earlier works: "The book is packed with interesting facts from the latest authorities, and the illustrations are happily chosen. Indices are all that could be desired."



L'AGRO ROMANO NEL PRIMO QUINQUENNIO FASCISTA. *Relazione sull'Incremento del Bonificamento Agrario e della Colonizzazione nell'Agro Romano dal 1° Gennaio 1923 (I) al 31 Dicembre 1927 (VI).*

Tipografia Cuggiani

20 lire

7¾ x 11¼; 191

Rome

This beautifully illustrated work shows what has been accomplished under the Fascist régime in improving agriculture in the Roman *campagna*. Tractor-driven

modern plows that break up the subsoil have replaced primitive ox-drawn plows; swamps have been drained and wells dug for irrigation. Modern cottages have replaced the thatched *capanne*, looking like a cross between a wigwam and a bee-hive, in which the peasants formerly dwelt. Schools and churches have been built, roads laid out, improved breeds of cattle and sheep introduced. Altogether this is an impressive testimony to what the Fascists have accomplished.



UNDERSTANDING WOMEN. *A Popular Study of the Question from Ancient Times to the Present Day.*

By K. A. Wieth-Knudsen (Translated from the Danish by Arthur G. Chater).

Elliot Holt

\$3.00 $5\frac{1}{2} \times 8$; xv + 324 New York

A masculine protest against the increasing ascendancy in the Western World of the female of the species. Dr. Wieth-Knudsen holds that woman has been overrated, that actually she is by physical constitution man's inferior, that she should submit to the facts, and as a corollary to the male. The data that the author offers in support of his arguments are not convincing, not even to an harassed male prejudiced in his favor.

Every cubic millimeter of man's blood contains half a million more red corpuscles than a cubic millimeter of woman's blood, and woman has relatively more water (80 per cent) in her blood than man (75 per cent). This is certainly one of the many peculiarities which by facilitating a more plentiful and rapid renewal of the bodily cells confer on man a greater mental power of resistance and a more enterprising spirit.

Just where the author obtained this information he does not tell, and we do not know. Frankly, we do not believe it is

true, and the same we may say for the similar statements that make up the rest of the book.



HUMAN NATURE AND HUMAN SURVIVAL. *An Essay.*

By Thiselton Mark. The Kingsgate Press
2s. 6d. net $5 \times 7\frac{1}{4}$; ix + 86 London

The author promises an argument in favor of after life and the supernatural which will be drawn from nature itself. The argument seems to be this: that man has grown up as part of the universe, of which more is knowable than known, is attuned to it, and has an instinctive impulse to reach out into it beyond the confines of his mundane life. This interpenetration with the universe requires more than ordinarily experienced nature, hence the supernatural, and more than ordinary existence, hence after life. It has several weak points; one is the premise that a wish for what is absent indicates that it exists somewhere.



PERSON UND MASSE. *Untersuchungen zur Grundlegung einer Massenpsychologie.*

By George Stielor. Felix Meiner Verlag
11 marks (paper) Leipzig
13 marks (bound)

$5\frac{3}{4} \times 9\frac{1}{4}$; 239

This is a systematic and interesting attempt to bring together and discuss critically what is known of group (social) psychology, approached from a general biological standpoint. The author takes the position that a scientific group biology is possible. The book is divided into three parts, of which the first deals with basic biological and psychological considerations and definitions. The second part discusses the relation of the individual to the group. Finally the third section treats of the group as such.

HINDU CUSTOMS IN BENGAL.

By *Basanta Coomar Bose.**The Book Company, Ltd.*1 rupee 4 $\frac{1}{2}$ x 7; 125 *Calcutta*

This account was originally written by a high caste Hindu in 1875 for the purpose of preserving records of the customs which were then prevalent among the Hindus in Bengal. Within the last fifty years, education among the upper classes has wrought many changes in the manner of living and the beliefs of the Hindus and many of the customs herein recorded are now obsolete. The author avoids, so far as possible, any discussion of religious beliefs, holding himself to an account of the customs connected with pregnancy, birth, infancy, adolescence, marriage and death.



AN INDEX TO THE ARABIC HISTORY OF GUJARAT. *Zafar Ul-Wálib Bi Muẓaffar Wa A'lib by Z' Abdalláh Muhammad Bin 'Omar Al-Makkí, Al-Aṣafí, Ulughkhání.* (Three volumes). *Being a List of Persons and Places Connected with the History of the Muslims in India Down to the Beginning of the Seventeenth Century.*

By *Sir E. Denison Ross.**John Murray (Published for the Government of India)*

7s. 6d. (for index)

*London*5 $\frac{1}{2}$ x 9; viii + 977

This is "perhaps the most extensive list that has hitherto been published of notable personages who lived during the domination of the Muslims in India from the Eleventh to the beginning of the Seventeenth Century." The list, however, is not limited to a mere enumeration of names. In the case of famous men, and frequently, in the case of less important individuals, a résumé is given of the important events in their lives. Thus much interesting information is now available

which otherwise could not be had until an English translation of the history appears.

JOHNS HOPKINS. *A Silhouette.*By *Helen Hopkins Thom.**The Johns Hopkins Press*\$2.75 6 x 9; xi + 125 *Baltimore*

Mrs. Thom calls her life of one of Baltimore's most distinguished citizens, a silhouette. It is indeed fortunate that a close bond of sympathy sprang up between the author, when a mere child, and her bachelor great-uncle. Else we might not have had preserved even this meager record of a man who brought into existence the Hospital and University which bear his name, and who provided so liberally (for his time) for their maintenance. Being a merchant and a banker, with no flair for putting his ideas in writing, Johns Hopkins left few manuscripts which could supply a background for a biography. Therefore we can know little of the ideas and plans of that quiet Quaker who played such a large part in the financial, charitable and educational affairs of Baltimore. Mrs. Thom does give us, however, a glimpse of some of the remarkable traits possessed by this unusual man.



OUR FOREFATHERS. *The Gothonic Nations. A Manual of the Ethnography of the Gothic, German, Dutch, Anglo-Saxon, Frisian and Scandinavian Peoples. Vol. I.*

By *Gudmund Schütte. Translated by Jean Young.**Cambridge University Press*

21 shillings

*London*6 $\frac{1}{2}$ x 9 $\frac{1}{2}$; xi + 288

The original of this volume appeared in Danish in 1926. The author's chief motive in writing the book was to supply a systematic framework for the study of

Anglo-Saxon ethnology "comparable to the German text-books of Zeuss, Brewer, Much and Kaufmann." Emphasis is put on "the strict regularity of plan" rather than on the subject matter, which is used mainly to illustrate the plan. Following the introductory chapter on "The Indo-Europeans" the arrangement of the sections is as follows: names, sub-division, ethnic position, environment, old home, language, civilization and history. The author has also sought to bring about a reform in nomenclature. There are frequent citations of literature throughout the text, an excellent index and a number of illustrations, chiefly distribution maps.

There is to be a second volume issued presently which will deal with the account of the individual Gothonic tribes and will follow the same general lines as volume one.



COLOR AT HOME AND ABROAD.

By George Mallison.

The Christopher Publishing House

\$3.00 5½ x 7½; 393 Boston

Mr. Mallison is "all het up" over the dangers of amalgamation of the whites and negroes in the United States and proposes as a prophylactic that the negroes shall be shipped back to Africa. This solution of the race problem was, if we remember rightly, tried nearly a century ago and met with no great success. When we reflect that the proportion of negroes and negro-white crosses in the population of the United States has decreased from 19.27 per cent in 1790 to 9.90 per cent in 1920, our blood refuses to boil at the thought of the future. When amalgamation comes—as it no doubt will by degrees—we see no likelihood that the national complexion will be darker than a light tan.

ADVENTURES OF AN OUTLAW. *The Memoirs of Ralph Rasbleigh, a Penal Exile in Australia 1825-1844.*

With Introductory Notes by Joseph W. Krutch and The Earl of Birkenhead.

Jonathan Cape and Harrison Smith
\$3.50 5½ x 8½; xxii + 349 New York

The book is an extraordinary human document, if true, and we are disposed to accept it as authentic, after a careful reading. The manuscript was sent to the publishers by Mr. Charles H. Bertie, the well-known librarian of Sydney, New South Wales. It is the story of an English convict transported to Australia for life as a convicted criminal, sometime in the early part of the nineteenth century. The picture of life in the Criminal Colonies which it paints is unforgettable. "Man's inhumanity to man" is notorious, and doubtless a century from now our present penological technique will seem as horrible as Australia's of 1830 does to us now, but perhaps a widespread reading of this book might help along a little. Every student of human behavior certainly should read it.



THE LIFE OF HERMANN M. BIGGS, M.D., D.SC., LL.D., *Physician and Statesman of the Public Health.*

By C.-E. A. Winslow.

Lea and Febiger

\$5.00 net

Philadelphia

6½ x 8½; xii + 432

A biography of the American pioneer in translating the bacteriological and immunological discoveries of the '80's and '90's into a public health program. Dr. Winslow is not one of the new style of biographers; his interest is as much in Biggs' professional work as in his personality. Nevertheless, from the mass of detail presented there emerges a clear view of the man as well as an interesting narrative of what he accomplished.

MAN AND CIVILIZATION: *An Inquiry into the Bases of Contemporary Life.*

By John Storck. Harcourt, Brace and Co.

\$3.75 5½ x 8½; v + 449 New York

An excellently written account of the biological, psychological, and sociological factors in civilization, intended for a college orientation course. The chapter on science contains one of the best brief treatments of scientific methodology that we know of. There are bibliographic notes at the end of each chapter and an index.



MAN AND SOCIAL ACHIEVEMENT.

An Introduction to Social Evolution.

By Donald C. Babcock.

Longmans, Green and Co.

\$3.00 5½ x 7½; xi + 546 New York

An account of how man came to be what he is in his social, economic, and other cultural activities. There is an appendix with questions for discussion, topics for investigation and readings on each chapter. There is also an index.



SOCIAL RESEARCH. *A Study in Methods of Gathering Data.*

By George A. Lundberg.

Longmans, Green and Co.

\$3.00 5½ x 7½; xi + 380. New York

A discussion of the planning of schedules, the carrying out of case studies, problems of terminology, units and classification and other questions involved in the gathering of data for the social sciences. There are a bibliography, a source list of social data, and author and subject indexes.



PAPAGO MUSIC. *Smithsonian Institution, Bureau of American Ethnology, Bulletin 90.*

By Frances Densmore.

U. S. Government Printing Office

\$1.25

Washington

5½ x 9; xx + 229

A record of the songs of a desert tribe of Indians living in Sonora, Mexico, and southern Arizona, and a description of the ceremonies in which these songs are used.



FAMILIENKUNDE. *Ihre Bedeutung und ihre Ziele.*

By Wilhelm Hussong.

Philipp Reclam

1.20 marks 3¼ x 6; 144 Leipzig

An interesting little contribution to human biology, of especial interest to eugenicists and social workers, since it reviews the whole subject of family study. There are 122 citations of literature.



THE GROWTH OF THE WORLD AND OF ITS INHABITANTS.

By H. H. Swinnerton.

Constable and Co., Ltd.

5 shillings 4½ x 7½; 211 London

This little book will be useful as collateral reading for beginners in natural science courses.



ZOOLOGY

ANTS AND THEIR RELATION TO APHIDS. *Bulletin 341.*

By Charles R. Jones.

Colorado Experiment Station

Free

Fort Collins

6 x 9; 96 (paper)

Some of the results of this investigation are as follows:

The relation between the ants of the *Formica* group and the aphids of the genus *Aphis* is a good example of mutualism. The ants of the genera *Lasius* and

Formica obtain a larger portion of their food from aphids than do the ants of other genera. The dissemination of aphids by ants is for the purpose of obtaining a greater production of honey-dew, this being accomplished when ants place the aphids on new tender growth where there is an abundance of sap. Aphids in their association with ants are very instrumental in transmitting plant diseases such as cucurbit wilt, fire blight and mosaic disease of sugar cane. An excess of honey-dew on the leaves of plants near large aphid colonies signifies a lack of sufficient ant attendants and is detrimental to the plant.

Included in the text are lists of Colorado ants and records of aphids attended; Colorado ants with the number of genera and species of aphids they attended; aphids with ant attendant; Aphid list with number of genera and species of ant attendants; ants associating together in aphid colonies; and mixed ants with genera and species associating together in aphid colonies. There is an extensive bibliography.



THE INDIAN ZOOLOGICAL MEMOIRS ON INDIAN ANIMAL TYPES. II. SCOLIODON (THE COMMON SHARK OF THE INDIAN SEAS).

By E. Muthammah Thillayampalam.

Lucknow University

2.8 rupees

Lucknow, India

6½ x 9½; xi + 116

There being no zoological text-books dealing especially with Indian types available, Indian universities and colleges have been obliged up to the present time, to use English books and laboratory manuals in their zoological courses. These, dealing with types mostly foreign, or at least not common, to India and Indian waters, require importation of specimens from great distances for laboratory use. In order to provide a means for studying the zoological types common to India, a series of monographs is being prepared. The present volume, belonging to this

group, substitutes *Scoliodon* (formerly known as *Carcharias*) the common shark of Indian waters, for *Scyllium* of European fame. The work includes sections on classification of Chondrichthyes, bionomics and distribution, external and internal characteristics, development, directions for laboratory work and a bibliography of 160 titles.



THE AVIFAUNA OF EMERYVILLE SHELLMOUND.

By Hildegard Howard.

University of California Press

\$1.25

Berkeley

7 x 10½; 86 + 4 plates (paper)

Out of something over 6700 bird bones collected from the mound, 4155 are identifiable. These represent 50 species of birds, of which 45 are found today in the San Francisco Bay region. The bones are in an excellent state of preservation. Usually the limb bones are broken into two or three pieces. This breakage probably occurred before the bones were thrown into the mound, many of them being charred at the broken ends. The age of the Emeryville mound is uncertain, but there seems to be no doubt that the latest date of occupation was prehistoric. From a study of the bird bones the author deduces a number of interesting facts concerning the habits of the Indians who inhabited this region while the mound was being formed. The book contains tables of bone measurements, and a table giving a comparison of the avifauna of Emeryville shell mound with recent and Pleistocene avifaunas.



THE FISHES OF OCEANIA. *Memoirs of the Bernice P. Bishop Museum. Volume X.* By Henry W. Fowler.

Bernice P. Bishop Museum
\$8.00 *Honolulu*

9½ x 12½; iii + 540 (paper)

Oceania comprises that extensive area in the tropical Pacific region, within which lie four principal faunal divisions: Melanesia, including New Guinea and Waigin; Micronesia; Polynesia, including Fiji; and Hawaii. The author of this memoir considers that he has herein described probably not more than half the species inhabiting these waters. Even so, an enormous amount of labor and care went into its preparation, as the large number of species listed and the detailed descriptions testify. The volume is issued in the same handsome form which characterizes all of the memoirs issued by the Bernice P. Bishop Museum of Honolulu. The plates, in monotone, convey a very definite idea of the distinguishing features of the specimens illustrated, if not of the brilliant coloring. There is an excellent index.



DIE RÄTSEL DES VOGELZUGES. Ihre Lösung aus experimentellem Wege durch Luftfahrt und Vogelberingung.
By Friedrich von Lucanus.

Hermann Beyer und Söhne
8.40 marks *Langensalza*

6½ x 9½; x + 266 (paper)

The third edition of a well known and extremely interesting treatise on bird migration, considered especially in its biological aspects. This edition brings the review of the literature up to date, and discusses the latest results from the bird banding experiments in various parts of the world. The author points out that there are now available data on the results of bird banding for 170 different species.



EINLEITUNG IN DIE PHYSIOLOG-

ISCHE ZOOLOGIE (Physikalische und Chemische Funktionen des Tierkörpers).

By Hans Przibram. *Franz Deuticke*
10 marks *Leipzig und Wien*

6½ x 9½; vi + 182 (paper)

A condensed digest of the literature of physiological zoology, using the term in the sense of chemical and physical aspects of animal function. The author expresses the hope that this book may serve the same function that his corresponding well known treatise has in the field of experimental morphology. The book is well indexed. In lieu of a detailed bibliography the author refers to a few well known large handbooks with full bibliographies.



INVESTIGATION OF THE PHYSICAL CONDITIONS CONTROLLING SPAWNING OF OYSTERS AND THE OCCURRENCE, DISTRIBUTION, AND SETTING OF OYSTER LARVAE IN MILFORD HARBOR, CONNECTICUT. *Bureau of Fisheries Document No. 1054.*

By Herbert F. Prytherch.

U. S. Government Printing Office
25 cents *Washington*

7½ x 11; 74 (paper)

The investigation here reported was directed to the elucidation of the physical conditions that affect oyster production in inshore waters. Included as factors studied are temperature, tide, salinity, hydrogen-ion concentration, and river discharge, and also biological observations on the condition of the gonads, time of spawning, occurrence and distribution of larvae and setting. A categorical summary and a bibliography are appended.



DIE TIERWELT DER NORD- UND OSTSEE. Lieferung XV.

Edited by G. Grinpe and E. Wagler

Akademische Verlagsgesellschaft m. b. H.
8.80 marks

Leipzig

6 x 8½; 108 (paper)

A taxonomic and briefly descriptive account of the following classes: *Aculifera* (Nierstrasz and Hoffmann), *Thalassobionte und thalassophile Myriapoda* (Schubart) and *Pisces*. It is part of a series intended as a comprehensive survey of the fauna of the North and Baltic Seas, a number of which have been previously noted in these columns.



DAS LEBEN DER SCHMETTERLINGE.

By Friedrich Schnack.

Jakob Hegner

7.50 marks (paper)

Hellerau

10.80 marks (bound)

5½ x 8½; 286

In America the popularity of the literary naturalist has declined since the days of John Burroughs; in Germany, apparently, he still flourishes. In this delightful book a novelist and poet, who is also an amateur of butterflies, tells us about some of the species and his adventures with them. The book is beautifully printed; our only wonder is that Herr Schnack did not use to illustrate it the skill in the painting of butterflies which he learned from the *Würzburger Glasermeister*.



HUMAN HELMINTHOLOGY. *A Manual for Clinicians, Sanitarians and Medical Zoologists.*

By E. C. Faust.

Lea and Febiger

\$8.00

Philadelphia

5½ x 9½; xxii + 616

An extensive discussion of the science of helminthology by one who has been for many years a teacher and investigator in this field. Much information is presented which has not been hitherto easily available. The book contains numerous

excellent illustrations and is well documented and indexed.



PRINCIPLES OF ANIMAL BIOLOGY.

By A. Franklin Shull, with the collaboration of George R. Larue and Alexander R. Rushven.

McGraw-Hill Book Co., Inc.

\$3.50 5½ x 9; xiv + 405 New York

A third edition, in which the chief changes from the former ones consist in an improvement of the chapter on genetics and of the portion devoted to the morphology and physiology of the higher types. We might ask, out of congenital captiousness, why exactly the same portrait of Gregor Mendel has to be reproduced twice, once on page 23 and again on page 226.



ALLGEMEINE VERGLEICHENDE PHYSIOLOGIE DER TIERE.

By H. J. Jordan.

Walter de Gruyter und Co.

32 marks (paper)

Berlin

34 marks (bound)

6¾ x 9½; xxvii + 761

An excellent treatise on the comparative physiology of animals which will be welcomed by all zoologists as a reference work. The standpoint is that of modern general physiology. The arrangement of the material is by a functional classification rather than taxonomic.



FRÜHFORMEN DER GEMEINSCHAFT IN DER TIERWELT.

By Friedrich Hempelmann.

Junker und Dünhaupt Verlag

1.30 marks 6½ x 9½; 23 (paper) Berlin

This is a reprint of a lecture on animal societies which formed one of a series on

social organization. It is an interesting popular summary of well known data from the literature of zoology.



PROPAGATION OF PONDFISHES.

Bureau of Fisheries Document No. 1056.

By M. C. James.

U. S. Government Printing Office

10 cents

Washington

5½ x 9½; 32 (paper)

The purpose of this report is to present briefly, essential facts related to the purpose of the rearing of pond fishes. It covers the propagation of basses, sunfish and catfish, and takes up questions of site, water, foods, etc., as well as relevant biological characters of the fish.



THE VENUS. *A Quarterly Journal Devoted to the Study of Mollusca.*

Published by The Malacological Society of Japan.

Tokubei Kuroda, Geological Institute, Science College, Kyoto Imperial University, Kyoto, Japan.

Subscription \$1.00 (Yen 2.20) per year, post-paid. 6 x 8½.



BOTANY

THE PLANT-LIFE OF THE BALKAN PENINSULA. *A Phytogeographical Study.*

By W. B. Turrill. Oxford University Press
\$10.00 (U. S. A.) New York and London
30 shillings net 6½ x 9½; xxiii + 490

An important contribution to studies in geobotany. The author has been singularly fortunate in the region which he selected for his investigation. In the Balkan Peninsula, which for a long geological period was either a part of Asia or

a broad isthmus connecting the Asiatic and European continents, there exists a unique flora. Within its boundaries are found plants which have drifted in from both the Asiatic and European regions; the altitude zones furnish a wide range in climatic conditions suitable for the growth of many varieties of plants; there are regions of primitive vegetation, undisturbed by man, similar to the plant covering of much of Europe in pre-glacial times; furthermore, there are many plant species which are indigenous to this region and are to be found nowhere else. Only the seed-bearing plants were studied, the investigator's aim being "to consider every aspect of the spermatophytic flora and vegetation that could throw light on the composition, origin, relationships, distribution, and successional changes of the plant-covering of the area."

Mr. Turrill has done his work with infinite pains and has produced a book of much interest. Of especial value is the analysis of the relation of the Balkan flora to that of the neighboring regions of Europe, Asia and Africa and the determination of the main lines of plant migration into and out of the Peninsula. Distribution tables of species, photographs of plants and of regions, and maps enhance the usefulness of the book. Unfortunately, lack of space prohibited the inclusion of the extensive list of titles dealing with plant life in the Balkans which the author has compiled. He gives, however, a group of selected references at the end of each chapter.



MICROBIOLOGY.

By B. F. Lutman.

McGraw-Hill Book Co., Inc.

\$4.00 5½ x 9; x + 495 New York

An excellent presentation of this subject.

The general plan is to discuss molds, yeasts, and bacteria as a group. The larger part of the book consists of descriptions of typical species. These types have been chosen "because they are common and have biological or practical importance, if possible, or both." When the type method cannot be followed satisfactorily, the author falls back on the plan of presenting common methods and results in general chapters. These he places at the beginning of the book and at the end.

The beginning (general) chapters are the author's solution of textbook work while a class is learning some elementary technic in the laboratory. The final chapters are an attempt to place before both teacher and student some of the theories, problems, difficulties, and controversies that confront the modern microbiologist. It has seemed well for the student to leave the subject not with the smug complacency that it is all neat, pat, and settled, but rather that he is looking out over a sea of boiling controversy and that many theories that he has been using may be discarded in another generation.

The book contains many excellent illustrations. Reference lists, frequently lengthy, conclude the different chapters. There is a detailed index.



A TEXTBOOK OF BOTANY.

By J. M. Lowson (*Revised in collaboration with the Author by L. C. Fox*).

University Tutorial Press, Ltd.

9 s. 6 d.

London

$4\frac{3}{4} \times 7\frac{1}{4}$; viii + 656

A seventh edition of a book which has been widely used in English institutions as a general introduction to the study of biology. Prepared to meet the requirements of a wide range of students, it deals in considerable detail with the various branches of the subject. Incorporated in the chapters on "Nutrition and growth" and the "Plant and its environment" is a

series of 76 experiments for class work. The work concludes with a section containing 152 test questions, an appendix in which many practical suggestions are given and an extensive index. In this edition, numerous changes have been made: obsolete technical terms have been deleted, the subject matter expanded, *Sphaerotheca* added as a type and the number of illustrations increased.



BOTANY. *Principles and Problems.*

By Edmund W. Sinnott.

McGraw-Hill Book Co., Inc.

\$3.00 $5\frac{1}{2} \times 9$; xxi + 441 New York

A second revised edition of a text-book for elementary work in botany, the essential idea of which is to arouse critical curiosity in the student's mind. Each chapter, after dealing briefly and concisely with the more important facts of the subject under discussion, concludes with lists of "Questions for thought and discussion" and "Reference problems." In all there are 747 in the former group and 238 in the latter. In this edition, the text has been largely rewritten, new material and illustrations added and the "Questions" and "Reference problems" revised considerably. Teachers of botany will find this an excellent book to place in the hands of their students.



THE STRENGTH OF NORTH AMERICAN WOODS. *United States Department of Agriculture Miscellaneous Publication No. 46.*

By H. S. Betts.

U. S. Government Printing Office

5 cents

Washington

$5\frac{1}{2} \times 9\frac{1}{2}$; 18 (paper)

The larger part of this paper consists of

a table giving the results of tests to determine the strength of various woods. Something over 125 varieties of wood are listed, while the properties of each, actual and comparative, are given under 21 headings. Among the various records may be mentioned weight per cubic foot (green, air dry, kiln dry); specific gravity, oven dry, based on volume when green; shrinkage from green to oven dry condition (in volume, radial, tangential); strength in bending; stiffness; hardness; etc. There are numerous explanatory notes.



MUSHROOMS OF FIELD AND WOOD.

By Margaret McKenny. The John Day Co.
\$2.00 5 x 7 $\frac{3}{8}$; xxiii + 193 New York

A handbook of the more common American mushrooms, illustrated with excellent photographs and with three color plates. There is a short bibliography and an index.



ACTA FORESTALIA FENNICA 33. Containing following articles: *Männyn Juuristo. Morfologinen Tutkimus.* (The Root System of Pine (*Pinus Silvestris*). A Morphological Investigation. Summary in English), by Erkki Laitakari; *Die Wurzelforschung in ihrer Beziehung zur Praktischen Forstwirtschaft*, by Erkki Laitakari; *Über Verhältnis der Winterfestigkeit des Roggens zur Dehnbarkeit und Dehnungsfestigkeit seiner Wurzeln.* (Summary in English. On the relation between the hibernation of rye and the tensile strength of its roots), by P. Kokkonen.

Society of Forestry in Suomi
Helsinki, Finland

6 $\frac{1}{2}$ x 9 $\frac{3}{8}$; 425 + 55 plates

ACTA FORESTALIA FENNICA 34.
AIMO KAARLO CAJANDER. 50-Vuotisjublauskaisu.

Commentationes in Honorem Professoris A. K. Cajander. Quinquagenarii Editae.

Society of Forestry in Suomi
Helsinki, Finland

6 $\frac{1}{2}$ x 9 $\frac{3}{8}$; 1006 + 31 plates



MORPHOLOGY

THE AUTONOMIC NERVOUS SYSTEM.

By Albert Kuntz.

Lea and Febiger

\$7.00

Philadelphia

5 $\frac{3}{4}$ x 9 $\frac{1}{4}$; xii + 576

In this general survey of a subject which is receiving an ever increasing amount of attention by the clinician and the surgeon, the author describes in a thoroughly comprehensive manner what is known to date concerning the autonomic nervous system. After a discussion of the morphology, physiology and development of the autonomic nervous system, he devotes much space to the innervation of the organs of the body. He then takes up pathological conditions. Visceral sensitivity and referred pain he treats in detail as well as the surgery of the autonomic nervous system. A lengthy bibliography (over sixty pages) adds greatly to the usefulness of the book. There is a group of well selected illustrations and an index.



BIOLOGIE DER GELENKE.

By Walther Müller.

Johann Ambrosius Barth

15 marks (paper)

Leipzig

17 marks (bound)

6 $\frac{3}{4}$ x 9 $\frac{3}{8}$; vii + 170

This is a thorough and useful discussion of the anatomy and physiology of joints, growing out of the author's investigations in the field of experimental orthopedics. The subjects treated are: the biology of joint cartilage; the biology of the joints;

arthritis deformans from the viewpoint of joint biology; the biology of the synovia and the joint capsule; the relation of the joints to the muscular, nervous, and endocrine systems; air pressure relations in joint regions. There is a bibliography of 10 pages and an adequate index. An excellent treatise on an interesting subject.



LEHRBUCH DER ENTWICKLUNGSGESCHICHTE. Fünfte, vollständig neu bearbeitete Auflage.

By Robert Bonnet herausgegeben von Dr. Karl Peter.

Paul Parey
Berlin

28 marks

6½ x 9½; x + 542

This fifth edition of Bonnet's textbook of embryology, which first appeared nearly a quarter of a century ago, has been almost completely rewritten by Dr. Peter, in order to bring it into accord with present day points of view. Its usefulness as an introductory text is thus ensured for another long period. There is appended a useful glossary of technical terms derived from Greek.



PHYSIOLOGY AND PATHOLOGY

THE PHYSIOLOGICAL MECHANICS OF PIANO TECHNIQUE. *An experimental study of the nature of muscular action as used in piano playing, and of the effects thereof upon the piano key and the piano tone.* By Otto Ortmann.

E. P. Dutton and Co., Inc.

\$6.50 5½ x 8½; xv + 395 New York

It is a rare thing to find combined in one person thorough training and competence as a professional musician, on the one hand, and equally thorough training and competence as a scientist, on the other

hand. This combination is exemplified, and indeed adorned, in the person of the author of this volume. Dr. Ortmann is the Director of the Peabody Conservatory of Music in Baltimore, a Hopkins Ph.D. in psychology, and, withal a scholar and an artist. In an earlier volume he has discussed the physics of piano playing. In the present one he treats of the physiology of that art. A third volume to deal with its psychology is promised. While perhaps merely the expression of a personal prejudice of the present reviewer, it is his opinion, for what it may be worth, that the ultimate valuation and permanent usefulness of this book will be as a contribution to physiology rather than to art. For obvious reasons physiology has, in the main, attempted to study only the simplest muscular movements. Here we have a courageous, and on the whole successful, attempt to analyze scientifically one of the most complicated, delicate, intricate, and highly coordinated and integrated sets of muscular movements that is known. In this attempt Dr. Ortmann has used standard physiological methods of recording, which, while not the most refined now available, are entirely adequate to his purpose. While thorough and painstaking, at times almost to the point of pedantry, the book is nevertheless extremely interesting, at least to the philosophical biologist. It is a fine, critical, intelligent piece of research. How the pianist will regard it we do not know. Probably chiefly as an exhibition book, to adorn the shelf and vicariously prove by its mere unread presence the intellectuality of the owner. Real musicians, bless their hearts, commonly enjoy exercising their fingers more than they do their brains.



PROGRESSIVE RELAXATION. *A Physiological and Clinical Investigation of*

Muscular States and their Significance in Psychology and Medical Practice.

By Edmund Jacobson.

University of Chicago Press

\$5.00 6 x 9; xiii + 429 Chicago

It is only fairly recently that what is certainly the most important factor, as well as one of the oldest known remedies, in the treatment of a vast number of bodily ills, has received careful, systematic study in the laboratory. The author of this book has devoted much time to an investigation of the purely physiological effects of rest on the human system and herein sums up the results of his work and gives a method for the application of what he terms "progressive relaxation" in the treatment of such cases as involve neuromuscular disorders. In progressive relaxation, suggestion or other psychotherapeutic measures play no part.

It is impossible to mention the many interesting details which this highly important work brings out. Its scope can best be indicated by giving some of the chapter headings: General features of neuromuscular hypertension; general features of progressive relaxation; the technic of progressive relaxation; the nature and technic of differential relaxation; the influence of relaxation upon the reflex reaction to sudden pain (flexion reflex); the influence of relaxation upon the knee-jerk; the influence of relaxation upon mental activities; the therapeutic use of relaxation, etc. In a section on "Explanatory Principles" the author gives some of the salient features of relaxation. Progressive relaxation is cultivated natural relaxation, a purely physiologic occurrence, which brings about a complete release of nervous tension. Learning to relax requires work on the part of the patient. He is instructed by his physician to do certain things in a particular way. He goes through the learning process by the

method of trial and error. Once his education is complete the patient can, on his own initiative, apply his skill in many ways towards a more rational way of conserving his nervous energy. Successful relaxation produces a feeling of well-being. It leads also to independence of manner and attitude; the longer the training, the greater on the whole becomes the independence.

This book will be extremely useful to the general practitioner, the surgeon and neurologist. It is well documented and contains author and subject indices.



LE PROBLÈME DES GLANDES À SÉCRÉTION INTERNE. *Les Propriétés physicochimiques et pharmacodynamiques des Hormones.* XII. I. L'Hypophyse.

By H. Penau, L. Blanchard and H. Simonnet.

Les Presses Universitaires de France

45 francs 6 x 9½; viii + 249 Paris

An excellent brief résumé of the present state of knowledge regarding the biological effects of the internal secretions from the two lobes of the pituitary body. The bibliography covers 25 closely printed pages and includes the literature up to January 1, 1928. The citations are not confined to French work, but the significant work which has been done in other countries is carefully reviewed, especially the American. The authors take a sane and conservative position regarding endocrinology generally, and are at pains to point out the silliness of what they call "endocrine fatalism," which would throw away our heredity, our intellectual faculties, our will, and our education. A useful book.



BAINBRIDGE AND MENZIES' ESSENTIALS OF PHYSIOLOGY. *Sixth Edition.* Edited and Revised by H. Hartridge.

Longmans, Green and Co.

\$5.00 5 $\frac{3}{8}$ x 8 $\frac{1}{2}$; xii + 528 New York

The primary object of this book was to meet the requirements of the medical student preparing for a pass examination in the subject of Physiology. Matter dealt with in laboratory text-books and all subjects of purely historical interest were excluded, so far as possible. In this edition, the sixth, the author has wrought many changes. New chapters have been written on basic principles, muscles, nerve, the central nervous system, vision, hearing, the liver, exercise and work. New sections have been added on capillary circulation, the vitamins, the kidney, etc. Many new diagrams have been substituted for those formerly used. One of the most useful features of the book is the carefully prepared index.



THE ORIGIN OF MALIGNANT TUMORS.

By Theodor Boveri (translated by Marcella Boveri). *The Williams and Wilkins Co.*

\$2.50 5 $\frac{1}{4}$ x 8; ix + 119 Baltimore

This treatise, by the late Theodor Boveri, appeared originally in Germany in 1914. The author summarizes his work in experimental cytology and discusses the relation which nuclear defects might have to malignant tumors. His conception is that "the cell of a malignant tumor is in some way a defective cell; it has lost some qualities of normal tissue-cells. . . . In this altered condition, the cell reacts differently to its surroundings, and this might be the sole cause of the tendency to unchecked cell multiplication." A "definite abnormal chromosome-complex" can explain certain characteristics of malignant tumors, among which are defective histological form and the altered biochemical behavior of tumor cells. The author suggests many lines of work in this

field which those who are studying the cytology of cancer will find interesting and valuable.



CEREBROSPINAL FLUID IN HEALTH AND DISEASE.

By Abraham Levinson. *C. V. Mosby Co.*

\$8.00 6 x 9; 386 St. Louis

A third edition of a highly useful book. It has been thoroughly revised to include all the recent important contributions on the subject. There has been a rearrangement of chapters so that the clinical sections are separated from the theoretical sections.



ANNALS OF THE PICKETT-THOMSON RESEARCH LABORATORY. Vol. V. *The Pathogenic Streptococci. Their Role in Human and Animal Disease (continued).*

The Williams and Wilkins Co.

\$10.00 Baltimore

8 $\frac{1}{2}$ x 11; xi + 392 (paper)



BIBLIOGRAPHY ON COD-LIVER OIL IN ANIMAL FEEDING with *Noncritical Comments and Abstracts.* Bureau of Fisheries Document No. 1065.

By John R. Manning.

U. S. Government Printing Office

10 cents

Washington

6 x 9 $\frac{1}{4}$; 33 (paper)



BIOCHEMISTRY

MECHANISM OF ENZYME ACTION AND ASSOCIATED CELL PHENOMENA.

By F. F. Nord.

The Williams and Wilkins Co.

\$2.00 5 $\frac{3}{4}$ x 9; ix + 78 *Baltimore*

This little book was written for the purpose of furnishing the student with a survey of certain phases of enzyme chemistry as a preliminary preparation for more detailed work in a highly complicated field. The author has succeeded admirably in giving a clear, concise presentation of the subject. He includes a bibliography of 189 titles. There is no index.



SEX

STERILIZATION FOR HUMAN BETTERMENT. *A Summary of Results of 6,000 Operations in California, 1909-1929.*

By E. S. Gosney and Paul Popenoe.

The Macmillan Co.

\$2.00 5 x 7 $\frac{3}{8}$; xviii + 202 *New York*

In this book is summarized the work which has been done prior to January 1, 1929, on the sterilization of defectives in California state hospitals. Much of the material included in this report has appeared at various times in technical journals. In all 6,255 individuals have been sterilized, a far larger number than have been so treated in any other single state where there are laws permitting sterilization. In fact, it is three times the total for all such states. The first part of the book gives a survey of the results of the sterilizations in the state hospitals, so far as it has been possible to follow up the individuals. The second part deals with general conclusions based on these studies and a consideration of the results of sterilization operations elsewhere. In the appendix there are nine chapters which deal with various phases of the subject, among which may be mentioned a list of technical papers on eugenic sterilization in California, an article on medical aspects of sterilization, by Dr. Robert L. Dickinson

of New York, and an outline of a state law providing for sterilization. Reginald, the Office Boy, says that the most important thing in the book—and perhaps he is right—is the statement that sterilization “has no effect upon sex desire, sex performance, or sex feeling of the subject, except a favorable psychological effect in some cases, particularly where the fear of pregnancy is removed.” But what of their prostates in the long run?



FACTORS IN THE SEX LIFE OF TWENTY-TWO HUNDRED WOMEN.

By Katharine Bement Davis. *Harper and Bros.*

\$3.50 6 x 9 $\frac{1}{4}$; xx + 430 *New York*

Realizing the need for more knowledge of the sex life of the normal individual, the Secretary of the Bureau of Social Hygiene here analyses the results of questionnaires obtained from 1000 married women and 1200 single women. The following subjects are treated: the use of contraceptives; frequency of intercourse as a possible factor in sterility; the happiness of married life; some auto-erotic practices; the periodicity of sex desire; homosexuality. We note from the table on “Sources of information as to contraceptive measures” that two women obtained their information from the Bible. This raises the interesting question whether it is not the duty of our customs authorities to exclude the Bible from this country, along with the works of Marie C. Stopes.



REPORT ON PHYSICIANS' REPLIES TO QUESTIONNAIRE CONCERNING THEIR EXPERIENCE WITH THE VAGINAL DIAPHRAGM AND JELLY.

Prepared by the Research Department of Holland-Rantos Co., Inc.

Sent on request.

New York

6 x 9; 27 (paper)

A high-toned piece of salesmanship, evidencing the progress of the world, on the one hand, and the need for further physiological research towards a perfect contraceptive, on the other hand.



A STUDY OF MASTURBATION AND THE PSYCHOSEXUAL LIFE.

By John F. W. Meagher.

William Wood and Co.

\$2.00 5 x 7 $\frac{3}{4}$; 130 New York

It is an encouraging sign that this temperately written book on a subject about which so much is popularly known "that ain't so" should reach a second edition. Dr. Meagher concludes that "the harm resulting from excessive indulgence in the habit is chiefly in the mental and moral spheres, rather than in the physical sphere." There are author and subject indexes.



THE PHYSIOLOGY OF LOVE.

By George M. Katsainos. The author

\$4.00 176 Huntington Ave., Boston
6 x 9 $\frac{1}{2}$; 326

The author, who appears to have hitherto written chiefly about syphilis, begins with the incontrovertible statement that "Man is a singular creature." The same remark may be made with equal justice about this book. It is an amazing *mélange* of autobiography, sexology, subtle eroticism, anti-feminism, metaphysics, and—so Reginald the Office Boy (who *will* surreptitiously read books which no pure young man should) says—blah. At the same time a cynical Pantagruelist will get an hour's amusement out of running through the book.

BIOMETRY

THE ADJUSTMENT OF ERRORS IN PRACTICAL SCIENCE.

By R. W. M. Gibbs. Oxford University Press

\$1.75 4 $\frac{3}{4}$ x 7; 112 New York

An excellent presentation of the theory of errors, simply and clearly written, and covering the normal curve of errors, area and volume distributions of errors, the method of least squares, the correlation coefficient, partial correlation, the correlation ratios, etc. The more mathematical portions have been isolated in an appendix, where there is no danger of their frightening the non-mathematical student.



FORTUNA or Chance and Design.

By Norwood Young.

E. P. Dutton and Co., Inc.

\$1.00 4 $\frac{1}{8}$ x 6; 93 New York

An entertaining account of roulette, horse racing and other devices for losing money easily and rapidly.



PSYCHOLOGY AND BEHAVIOR

FEELINGS AND EMOTIONS. The Wittenberg Symposium.

By Thirty-four Psychologists, edited by Martin

L. Reymer. Clark University Press

\$6.00 6 x 9; 454 Worcester

In this book are printed the papers given by various eminent psychologists at the symposium held on the occasion of the inauguration of the new Psychological Laboratory of Wittenberg College, Springfield, Ohio. Dr. Cattell, a competent judge, doubts "whether there has ever been held a meeting of psychologists in which were presented so many papers of such high average merit." The papers of the symposium are as follows: Is "emo-

tion" more than a chapter heading? by Madison Bentley; The place of emotion in modern psychology, by Joseph Jastrow; A new method for investigating the springs of action, by Charles E. Spearman; Emotion, conation, and will, by F. Aveling; The essence of feeling: outline of a systematic theory, by F. Krueger; The feeling-tone of sensation, by F. Kiesow; Emotion and thought: a motor theory of their relations, by Margaret F. Washburn; The utility of emotions, by W. B. Pillsbury; Feelings and emotions, by Ed. Claparède; A functional theory of the emotions, by D. T. Howard; Emotion as a dynamic background, by Knight Dunlap; Can emotion be regarded as energy? by Morton Prince; Feeling and emotion as forms of behavior, by Albert P. Weiss; Displeasure and pleasure in relation to activity, by Karl Bühler; Emotion and feeling distinguished, by William McDougall; Phonophotography as a new approach to the psychology of emotion, by Carl E. Seashore; Excitement as an undifferentiated emotion, by George M. Stratton; How emotions are identified and classified, by Robert S. Woodworth; The differentia of an emotion, by Harvey A. Carr; Pleasantness and unpleasantness as modes of bodily experience, by L. B. Hoisington; Pleasurable reactions to tactual stimuli, by Robert H. Gault; Neural organization for emotional expression, by Walter B. Cannon; Emotions as somato-mimetic reflexes, by Vladimir M. Bekhterev; Emotion in animals and man, by Henri Piéron; Fear of action as an essential element in the sentiment of melancholia, by Pierre Janet; A theory of elements in the emotions, by Carl Jørgensen; Feelings and emotions from the standpoint of individual psychology, by Alfred Adler; "Ernstspiel" and the affective life: a contribution to the psychology of personality, by Wilhelm Stern; The development of conscience in the child as revealed by his talks with

adults, by David Katz; The rôle of feeling and emotion in aesthetics, by Herbert S. Langfeld; Psychological and psychophysical investigations of types in their relation to the psychology of religion, by Erich Jaensch; Feelings and emotions in the psychology of religion, by D. Werner Gruehn; Historical development of the theory of emotions, by G. S. Brett; Training the emotions, by John S. Terry.



AN INTRODUCTION TO THE STUDY OF BIRD BEHAVIOR.

By H. Eliot Howard.

Cambridge University Press
£2, 2s. 9½ x 12½; xii + 136 London
\$14.00 The Macmillan Company
New York

Mr. H. Eliot Howard is well known from his earlier studies in bird behavior. The present volume will substantially add to his reputation. It embodies a thorough-going observational and experimental study of the breeding behavior of, first, a reed-bunting, *Emberiza schoeniclus schoeniclus*, and, second, a yellow-bunting, *Emberiza citrinella citrinella*. The record of the observational work in the field bears in every line the marks of unhurried thoroughness, precision, exactness, penetration and understanding. The two observational chapters are followed by longer chapters analyzing the behavior into its components. The two final chapters attempt a synthesis under the attractive headings "The Whole Has Value, the Parts by Themselves have None," and "An Approach to a Mind Story." The general conclusion reached is against the behaviorist position of Watson and in favor of cognitive reference and revival in the form of imagery. The book is beautifully printed and illustrated, and is a contribution to animal psychology of first-rate importance.

REASONING IN WHITE RATS.

By Norman R. F. Maier.

The Johns Hopkins Press

\$1.75 7 x 10½; 93 (paper) Baltimore

Lack of space permits only a few of the results of this interesting series of experiments on reasoning in rats to be given. The author found that:

Rats can combine the essential relations of one situation with those of another in such a way as to reach the goal which could not be reached by any one concrete experience. They can adequately adjust themselves to a new situation without "trial and error," but with intelligence and insight.

The behavior of a rat varies for the same situation. The end determines the response and the means to the end may vary.

A rat can select the shorter of several routes to food in a known situation without first going over them in connection with food or in any special and invariable order.

The knowledge of a situation is spatial and not a series of successive experiences for the rat. When the rat is familiar with a situation, it knows it as an immediate whole.



A STUDY OF THE RELATIONSHIP BETWEEN THE INTELLIGENCE AND MORAL JUDGMENTS OF COLLEGE STUDENTS. *Peabody Contributions to Education No. 51.*

By Paul L. Boynton.

George Peabody College for Teachers

75 cents 6 x 9; 49 (paper) Nashville

The subjects were 243 students, 120 girls and 123 boys. The criteria of intelligence were Army Alpha scores or other tests translated into these. The criteria of moral judgment consisted of scores set down by the subjects as to the moral heinousness of lapses in such matters as Sunday observance, taking life, use of stimulants, etc.; when no wrong was considered involved a mark of 0 was assigned, when an act was as wrong as could be, a mark of 10. Thus a low score indicated

moral leniency, a high score moral stringency. The outstanding characteristics of the results is that there is a lack of relation between intelligence and moral judgment, although there does appear to be a weak tendency for high intelligence to be accompanied by relatively lenient judgment.



THE THINKING MACHINE.

By C. Judson Herrick.

The University of Chicago Press

\$3.00 5 x 7½; xii + 374 Chicago

A clear and interesting account for the general reader of neurology, and of psychology from a neurological standpoint. The trouble with most mechanistic treatments of biology and psychology, Dr. Herrick finds, is that they do not take a wide enough view of the nature of a machine. By enlarging the conception of a machine to include everything that performs work by natural agencies in accordance with natural laws, he finds that all life, including the mental or spiritual life, is a mechanistic process and can be explored by the scientific method.



DIE PSYCHISCHEN REAKTIONSFORMEN.

By Harry Marcuse.

S. Karger

22 marks 7 x 10½; 262

Berlin

This is an attempt to demonstrate the practical application of Jasper's "energetic theory of psychoses" by examples drawn from the clinic and the laboratory. The treatment is broadly biological, and the book will interest psychologists and students of behavior generally. Its usefulness is diminished by the lack of an index.

THE COMMON SENSE OF DREAMS.

By Henry J. Watt. Clark University Press
\$3.00 6 x 9; xvii + 212 Worcester

A Scotch psychologist, who thinks there is something in psychoanalysis but is repelled by the vagueness and mysticism of its technique, develops in this book a simpler and less fantastic scheme for the interpretation of dreams.

DE OMNIBUS REBUS
ET QUIBUSDEM ALIIS

THE SCOTS KITCHEN. *Its Traditions and Lore with Old-Time Recipes.*

By F. Marian McNeill.

Blackie and Son (Canada), Ltd.
\$2.25 5½ x 7½; xvi + 259 Toronto

This delightful book gives not only a great many old Scottish recipes (something over 260 in all) but includes much that is interesting pertaining to the history of Scottish social life. If any one supposes that the Scots of old lived solely on the coarser varieties of food, he has only to glance through this book to be otherwise convinced. Numerous recipes are most alluring. As a random sample we give the following: Partan Bree (crab soup), Lobster-Haut Goût, Roast Grouse, Haggis Royal, Scots Apple Pudding, Whim-Wham, and Scots Woodcock. Kings and noblemen, especially during Edinburgh's golden age, had French cooks, and they undoubtedly influenced Scottish cuisine to a considerable extent. Many of the fine old recipes, however, originated in the cottage kitchen. In the appendix there are sections on Franco-Scottish domestic terms, old Scottish measures, old Scottish festival cakes and dishes, and sources of recipes. There is an index of recipes.

SCIENCE AND THOUGHT IN THE FIFTEENTH CENTURY. *Studies in the History of Medicine and Surgery, Natural and Mathematical Science, Philosophy and Politics.*
By Lynn Thorndike.

Columbia University Press
\$4.75 5½ x 9; xii + 387 New York

Probably no period in the history of civilization is so bound in summary generalities as the Middle Ages, of which it has been said that they are called dark because we know so little about them. The monumental researches of this author as exemplified in his *History of Magic and Experimental Science* and this volume will go far to establish a more authentic view of those formative centuries than we now have. Contrast the glib assurances of our text books with the caution of the scholar; "It is hardly possible as yet to draw a general picture of fifteenth century thought and science." Like the earlier work mentioned this is no comprehensive history, but rather a source book to which future general historians will turn for enlightenment. It consists of special studies in the science and thought of the fifteenth century based on manuscript and unpublished materials. A great learning went into its making and a great industry.



MYSTICISM AND LOGIC.

By Bertrand Russell.

W. W. Norton and Co., Inc.
\$3.00 5½ x 8½; 234 New York

Another volume in the popular priced reeditions of Russell's works which are being issued from this press. It contains some of the philosopher's most readable and oft-quoted essays. "Mathematics and the metaphysicians" is there and so is "A Free Man's Worship." In a new introduction which the author prepared

for this edition he declares certain changes from the philosophic position taken when the work was first written some fifteen years ago. One gathers from his remarks that Mr. Russell is now a good deal of a pragmatist.



A HANDBOOK ON HANGING. *Being a short Introduction to the fine art of Execution, and containing much useful information on Neck-Breaking, Throttling, Strangling, Asphyxiation, Decapitation and Electrocutation; as well as Data and Wrinkles for Hangmen, an account of the late Mr. Berry's method of Kill-*

ing and his working list of Drops; to which is added a Hangman's Ready Reckoner and certain other items of interest. All very proper to be read and kept in every family.

By Charles Duff. Hale, Cushman and Flint
\$1.50 4 x 6½; 130 Boston

A satire directed against capital punishment. It takes the form of a defense of the hangman as an artist worthy of more attention and respect than he now gets. It is only mildly amusing in its humorous portions and where it is meant to horrify, is too refined, we are afraid, to shock a public hardened as we are by tales of the late war.



THE QUARTERLY REVIEW of BIOLOGY



THE FOOT MUSCULATURE OF THE HIGHLAND GORILLA (*GORILLA BERINGEI*)

By WILLIAM L. STRAUS, JR.

Department of Anatomy, Johns Hopkins University

THE musculature of the gorilla foot is fairly well known. It has received the attention of a number of investigators. Some of these workers have, however, confined their attentions to specific muscles, while others have described in detail only those muscles which differed markedly from the usual condition in man. Most striking perhaps is the lack of adequate illustrations (except in the beautifully illustrated monograph of Duvernoy). In connection with studies on Primate feet, I recently was able, through the courtesy of Dr. William K. Gregory of the American Museum of Natural History, to dissect the right foot of an adult female highland gorilla, of the species *Gorilla beringei* (Amer. Mus. Nat. Hist., Compar. Anat. No. 47). This foot was obtained in East Africa by the late Carl Akeley.

I believe that I am correct in affirming this to be the first description of the complete foot musculature of the highland gorilla of East Africa. Morton (1924) studied the left foot of the animal described herein, but his account is confined to a description of the *M. peroneus tertius*. My assumption is based upon the date of dis-

covery of *Gorilla beringei*. This highland form of gorilla was first made known in 1901 by von Beringe, hence its name (Derscheid, 1927). There is therefore no doubt that the specimens of gorilla described prior to this data are of the lowland type, *Gorilla gorilla*. My search of the literature has yielded four accounts since 1901 which consider the muscles of the gorilla foot. The gorilla dissected by Sommer (1906) is without doubt of the species *G. gorilla* (see Schultz, 1927). That studied by Pira (1913-14) was from the French Congo, and was almost certainly *G. gorilla*, since *G. beringei* is not known to occur in that area. The infantile gorillas of the Zürich collection in which Loth (1908) described the *aponeurosis plantaris* and Sawalischin (1911) the *M. flexor digitorum brevis*, are definitely stated by these authors to be specimens of *G. gorilla*.

Although the highland gorilla has been denied the rank of a separate species by some authors (e.g., Derscheid and Coolidge, both of whom regard it as merely a subspecies of *Gorilla gorilla*, and designate it *Gorilla gorilla beringei*), there is evidence which indicates that it differs considerably

from the West African or lowland gorilla (*Gorilla gorilla*), particularly in the outer form of the foot and hand, and in the proportions of the limb bones (Schultz, 1927). The foot of the highland gorilla seems to be relatively broader than that of the lowland form; the heel is broader and better developed; the great toe is relatively longer, and the free digital length much less. This naturally leads us to the question: Does the highland gorilla differ from the lowland gorilla in the structure and arrangement of the muscles of the foot, and if so, to what degree? I shall attempt to throw light upon this question, in so far as the very limited amount of material permits.

The literature dealing with the foot muscles of *Gorilla gorilla* has been indispensable in this study, because it has made it possible for me to compare that species with *G. beringei* and to consider the known range of variation. I have not, however, attempted to consider fully the papers dealing with other Primates. In addition to the foot of the *G. beringei* upon which this study is based, I have had the opportunity of making certain observations upon an infant female *G. gorilla* (Amer. Mus. Nat. Hist., Comp. Anat. #1105) dissected by Dr. Dudley J. Morton. Furthermore, I have studied the pedal interosseous muscles of a juvenile female *G. beringei* (Coll. of Labor. of Phys. Anthropol., Johns Hopkins University, #7) and an infant female *G. gorilla* (Coll. of Labor. of Phys. Anthropol., Johns Hopkins University, #5). Specimens of additional Primates dissected by me in connection with other work will also be referred to from time to time.

These specimens are as follows: left foot of a juvenile male chimpanzee (*Pan chimpanse*), #162; left foot of a juvenile male orang-utan (*Pongo pygmaeus*), #37; left foot of an adult female gray gibbon (*Hylobates pileatus*), #133; right foot of an adult langur (*Pygathrix germaini*), #134; and left foot of an adult galago (*Galago* (sp.?)), #221436. The first four specimens are from the collection of the Department of Anatomy, Johns Hopkins University. The chimpanzee and orang feet (#162 and #37) are from animals which are being dissected in this laboratory by Mr. T. D. Stewart. The galago is from the Division of Mammals, U. S. National Museum.

I wish to thank Dr. W. K. Gregory for the unique

opportunity of studying the foot of the adult *G. beringei*, and for allowing me to examine the dissection of the young *G. gorilla* made by Dr. D. J. Morton. I also wish to thank Dr. Morton, who very obligingly permitted me to study his dissection. In addition thanks are due Mr. Gerrit S. Miller, Jr., for the opportunity of dissecting the specimen of *Galago*.

I have considered it necessary in this study to ascertain the innervation of the muscles, whenever possible, because of the clues given thereby to the identification of certain muscles and their elements. This is particularly important in a consideration of the deep plantar musculature, where it sometimes becomes necessary, as in the specimen of *G. beringei* under consideration, to decide whether the outer (fibular) head of the *M. flexor hallucis brevis* is completely absent or whether it has become incorporated in the *M. adductor hallucis*. Such a question can be decided only by recourse to the innervation. Homology based upon innervation necessarily is a consequence of the acceptance of the hypothesis of Fürbringer (1888), which assumes a constant relationship between peripheral nerve and striated muscle throughout development. An excellent exposition of this hypothesis, with examples from the facialis musculature, has been given by Huber (1925).

In a relatively simple nerve such as the facial, the nerve-muscle relation, as Huber has shown, seems well-established. But when dealing with the limb-plexuses, the theory apparently is open to exceptions. Such apparent exceptions have been dealt with, for example, by Cunningham (1882). The limb-plexuses are of such complex structure that it is next to impossible to decide whether the exceptions to the Fürbringer hypothesis are real or apparent. Confining myself merely to the foot, I desire to discuss a few muscles that exhibit inconstant nerve-supply, as every anatomist knows. The *lumbricales*, particu-

larly those for the third and fourth toes, may at times be innervated by the medial plantar nerve, at times by the lateral, and occasionally by both. This may be explained by discarding the Fürbringer hypothesis and by considering that the muscle areas supplied by the plantar nerves are not sharply defined, or by assuming the possibility of a heterotopic or secondary innervation. On the other hand, an explanation may be offered on the basis of the nerve-muscle hypothesis. It is of course possible that in such a complicated arrangement as a limb-plexus, nerve-fibres may not always follow their accustomed paths. Therefore, fibres nominally belonging to one plantar nerve may sometimes be carried with those of the other plantar nerve. Muscles may therefore receive an innervation that is macroscopically anomalous, or the innervation may seem to vary, whereas it actually does not. Again, wherever the muscle fields supplied by two nerves lie so close together, as in the case of the plantar nerves, there is always the strong possibility, even probability, that certain muscles on or near the boundary line may at times be derived from the muscle anlagen supplied by one nerve, at times from the muscle anlagen of the other nerve. This last reasoning could apply not only to the *lumbricales*, but also to the *M. flexor digitorum brevis pedis*. This muscle is usually innervated by the medial plantar nerve alone. Not infrequently, however, in addition to its usual nerve, a twig from the lateral plantar nerve may enter the outer border of the muscle, supplying the portion of the belly which gives rise to the tendon for the fifth toe. There is no need to regard this as due to secondary innervation; it may be explained by assuming that the lateral portion of the muscle may at times be derived from the field of the lateral plantar nerve. Similar explanations, on the basis of the Für-

bringer hypothesis, can be given for the occasional branch from the lateral plantar nerve to the fibular head of the *M. flexor hallucis brevis*, or the occasional medial plantar twig to the oblique head of the *M. adductor hallucis*, both of which conditions may occur in otherwise normal feet. At the lateral margin of the great toe the fields of the two plantar nerves lie close together. It is therefore not difficult to believe that the flexor sometimes contains muscle-fibres from the lateral plantar anlagen, and the adductor occasionally from the medial plantar anlagen. These two muscles, in particular, may exhibit varying degrees of fusion (orang-utan of Ruge (1878b), gorilla of Straus), a further indication of the instability of this muscle area. Without necessarily assuming that the Fürbringer hypothesis is an established fact, and despite its very definite limitations, especially when working with the nerves of the limb-plexuses, this idea is nevertheless the best guide in homologizing muscles at the present time. It is of tremendous value in phylogenetic investigations. I have therefore applied this principle of nerve-muscle relationship in my work, although I fully realize that it must always be used with reservation, especially in the extremities.

DESCRIPTION OF MUSCLES OF FOOT OF THE
ADULT FEMALE (# 47) GORILLA
BERINGEI

The foot was skinned in the field by Mr. Akeley, and it was removed from the leg at the ankle joint. I was therefore unable to study the origins and innervations of the muscles which arise outside of the foot itself, nor am I able to discuss the cutaneous innervation. A brief preliminary report of the foot musculature of this specimen has already been published (see Straus, 1929a).

Muscles of the Sole

Aponeurosis plantaris (fig. 1). This arises from the *tuber calcanei* and extends forward over the middle of the foot to the region about the heads of the metatarsals. Although the part of the aponeurosis over the body and base of the second and the body of the third metatarsals had, unfortunately, been removed in the skinning, the essential details could be made out.

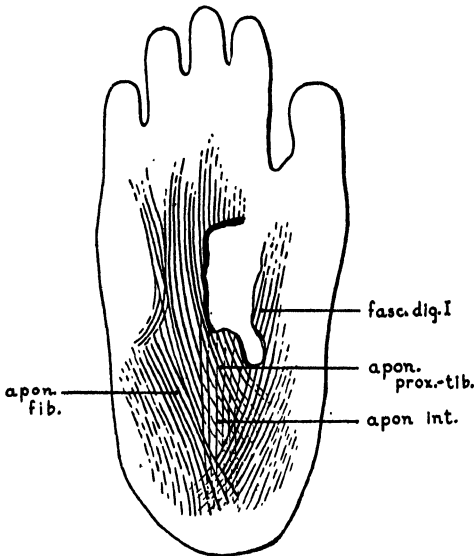


FIG. 1. GORILLA BERINGEI (No. 47). PLANTAR APONEUROSIS

apon. fib. = aponeurosis fibularis; *apon. int.* = aponeurosis intermedialis; *apon. prox.-tib.* = aponeurosis proximo-tibialis; *fasc. dig. I* = fasciculus digiti I. \times approx. $\frac{1}{10}$ natural size.

There is a definite *aponeurosis intermedialis*, crossed at about the middle of the sole by the *aponeurosis tibialis proximo-medialis*, which in turn is crossed above by the *fasciculus digiti I*. The outer portion of the *aponeurosis fibularis* stops at about the end of the tarsus, over the *abductor digiti V*, where it thins out, the remainder running toward the digital region; it has a strong attachment to the base of the fifth metatarsal. The *fasciculus digiti I* thins out

over the proximal part of the belly of the *abductor hallucis*. There are strong, deep processes from the fibular side of the aponeurosis. All of the various elements of the aponeurosis mingle in the region of the heel. The greatest thickness is over heel and tarsus (about 3 mm. over the former).

M. abductor hallucis (figs. 2, 4, 9, 10). This is a large and powerful muscle, arising from the medial process of the *tuber calcanei*, the lacinate ligament and under surface of the plantar aponeurosis. The lateral fibres of origin mingle with those of the *flexor digitorum brevis*. The powerful muscle-belly is prolonged as a flat tendon, to which are joined, on each side, the fibres of the tibial (inner) head of the *flexor hallucis brevis*, and which is inserted into the medial side of the base of the basal phalanx of the hallux and the metatarso-phalangeal joint capsule of that toe. *Innervation*: by a branch from the main trunk of the medial plantar nerve.

M. abductor digiti V (figs. 2, 3, 4). This is a well-developed muscle, arising chiefly from the plantar and lateral surfaces of the *tuber calcanei*, as far lateral as the *processus peroneus* (see Weidenreich, 1922), with an additional origin from the under surface of the plantar aponeurosis. The most medial fibres of origin touch those of the superficial head of the *flexor digitorum brevis*. The more lateral fibres, arising from the *processus peroneus* and lateral surface of the calcaneus, split off from the main mass of muscle not far beyond their origin and insert fleshily into the tuberosity of the fifth metatarsal bone, forming a *M. abductor ossis metatarsi V* (figs. 2, 3). The rest of the muscle is prolonged into a tendon which pierces the muscle mass of the *flexor digiti V brevis*, lying between the superficial and deep layers of the latter, and inserts into the fibular side of the base of the basal phalanx of the fifth toe.

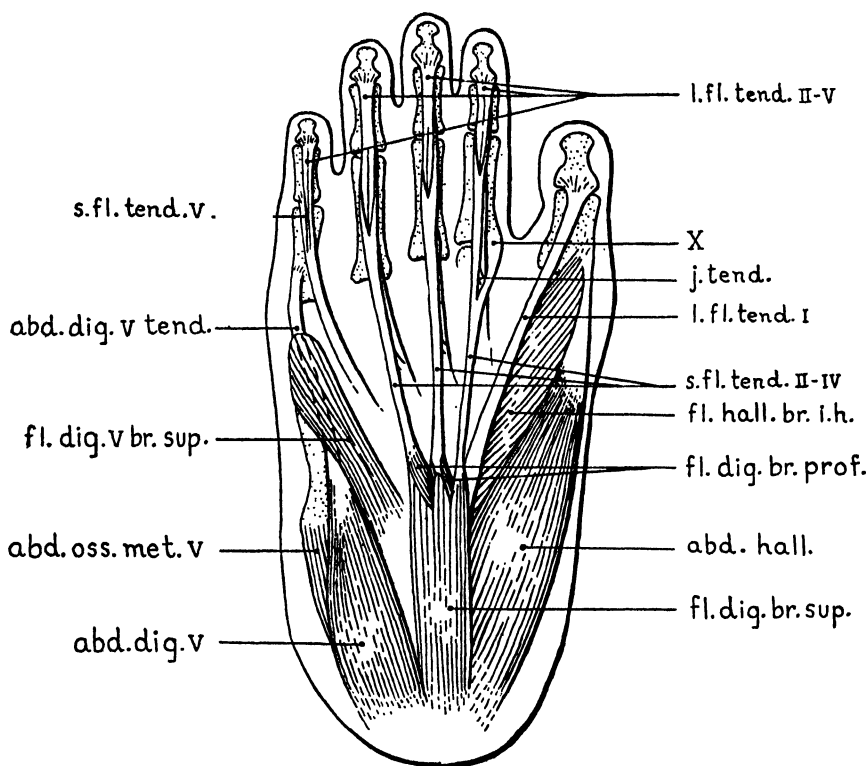


FIG. 2. GORILLA BERINGEI (No. 47). SUPERFICIAL PLANTAR MUSCLES

abd. dig. V = abductor digiti V; *abd. hall.* = abductor hallucis; *abd. oss. met. V* = abductor ossis metatarsi V; *fl. dig. br. prof.* = deep head of flexor digitorum brevis; *fl. dig. br. sup.* = superficial head of flexor digitorum brevis; *fl. dig. V br. sup.* = superficial layer of flexor digiti V brevis; *fl. hall. br. i. h.* = tibial head of flexor hallucis brevis; *j. tend.* = vincula; *l. fl. tend.* = long flexor tendon; *s. fl. tend.* = short flexor tendon; X = tendinous slip from short flexor tendon II to second metatarso-phalangeal joint. X approx. $\frac{1}{2}$ natural size.

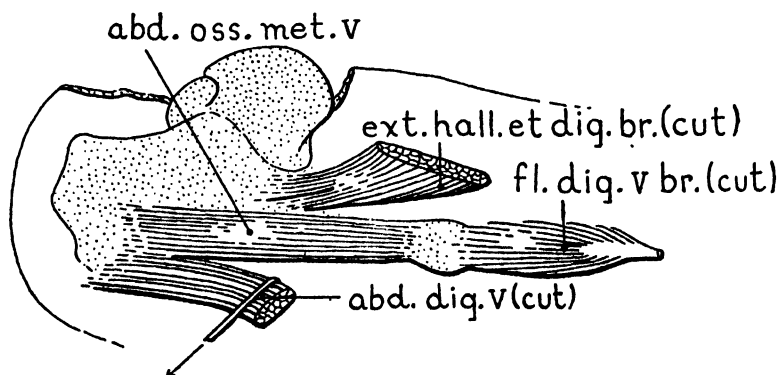


FIG. 3. GORILLA BERINGEI (No. 47). LATERAL VIEW OF FOOT

abd. dig. V = abductor digiti V; *abd. oss. met. V* = abductor ossis metatarsi V; *ext. hall. et dig. br.* = short extensors; *fl. dig. V br.* = flexor digiti V brevis. X approx. $\frac{1}{2}$ natural size.

Innervation: the main belly receives a branch from the main trunk of the lateral plantar nerve. I could find no separate nerve for the part forming the *abductor ossis metatarsi V*; no doubt it receives its fibres from the nerve which innervates the *abductor digiti V*.

M. flexor digitorum brevis (figs. 2, 4, 5, 7, 15). This muscle is composed of two distinct heads of origin, which, when observed from the plantar surface, may be called "superficial" and "deep," respectively. The superficial head arises chiefly from the medial process of the *tuber calcanei* and in a lesser degree from the under surface of the plantar aponeurosis; the fibres mingle medially with those of the *abductor hallucis*, and touch laterally those of the *abductor digiti V*. This head provides a perforated tendon for the second toe, about half of the perforated tendon for the third toe, and most of the perforated tendon for the fourth toe. The deep head, which is much smaller than the superficial, arises from the plantar surface of the undivided tendon of the *flexor tibialis* before the latter joins the tendon of the *flexor fibularis*. This head is fleshy on its plantar aspect. It must have extended up into the leg, for at the ankle, where the muscle has been severed, it is quite robust and clearly has a higher origin. The deep head gives off two fleshy bellies, the medial of which supplies about half of the perforated tendon of the third toe, while the lateral contributes to the formation of the perforated tendon of the fourth toe. There is no true short flexor tendon for the fifth digit, but what I should consider a vestige of this structure arises from the terminal tendon of the *flexor fibularis* for toe V, and is discussed with that muscle (fig. 2). The short tendons for the third and fourth toes are perforated, as in man, by the long flexor tendons of those digits, this perforation occurring at about the middle or

distal half of the basal phalanges. Only a portion of the short flexor tendon for the second toe goes as a perforated tendon to that toe; a large part inserts by a broad tendinous expansion into the plantar and tibial surfaces of the head of the second metatarsal bone and the metatarso-phalangeal joint-capsule of that ray. The short flexor tendons, prior to their perforation, lie plantar to those of the long flexor. Afterwards they lie dorsal to the latter. Following perforation the halves of each short flexor tendon reunite, but shortly thereafter each divides once more and inserts into the approximate middle of its respective middle phalanx by two processes, one on each border of the bone (fig. 7). The tendons are united to those of the long flexors by vincula, which are, however, not always well-developed (figs. 2, 4, 7). *Innervation:* the superficial head receives two branches from the main trunk of the medial plantar nerve. I failed to find any nerve supplying the deep head. I suspect that this portion of the muscle receives its nerve above the ankle, for the muscle fibres, as I have previously mentioned, show definite signs of having a higher extension. Such a nerve may have come directly from the tibial nerve, or else from one of the plantar nerves, which are already distinct at their points of severance in the ankle, thus indicating that the tibial nerve divided into the two plantar nerves quite high up in this specimen.

Origin of tendons of M. flexor digitorum brevis

Superficial head:

to toes—2 3 4

Deep head

to toes— 3 (4) (5 vestige)

(In this and similar tables, where an end tendon receives contributions from two sources, that part of the tendon which supplies the minor portion is enclosed by parentheses. When there are two sources,

and neither figure is enclosed by parentheses, the author has given no information concerning the relative contribution of each source, or else, as in the above table, the contributions are equal.)

M. flexor tibialis (= *M. flexor digitorum longus*) (figs. 2, 4, 6, 7, 15). Although the origin of this muscle is not present in the

tibial flexor lies slightly superficial to that of the *flexor fibularis*, with which it unites to form a broad common tendon. A careful dissection and tracing of the fibres in the common tendon formed by the tibial and fibular flexors leaves no doubt concerning the sources of the long flexor

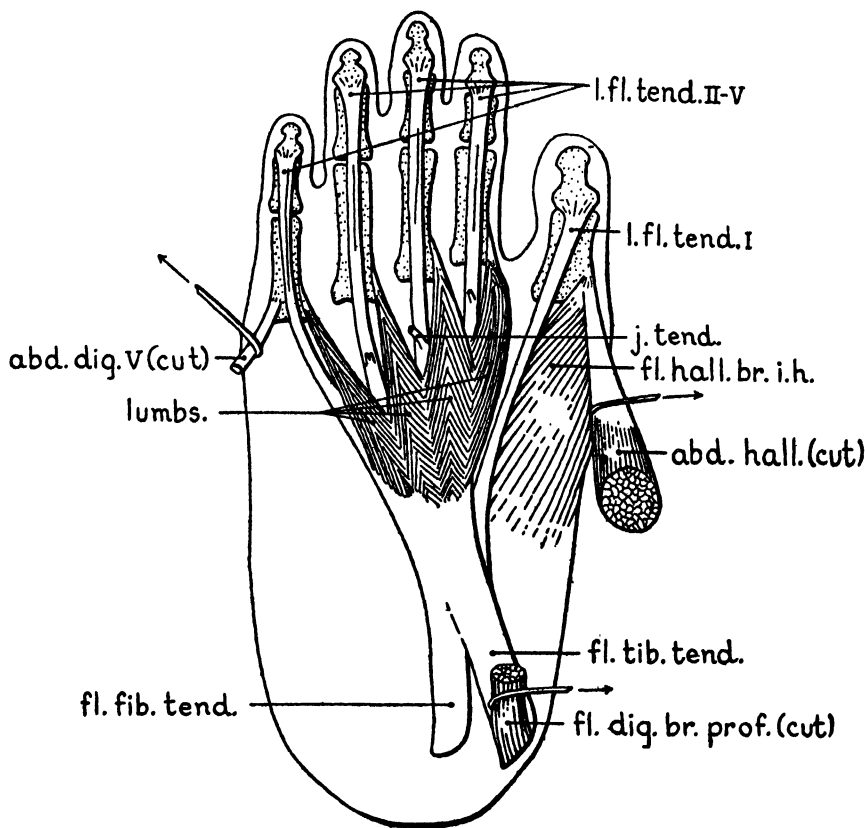


FIG. 4. GORILLA BERINGEI (No. 47). LONG FLEXOR TENDONS AND LUMBRICALES

abd. dig. V = abductor digiti V; *abd. hall.* = abductor hallucis; *fl. dig. br. prof.* = deep head of flexor digitorum brevis; *fl. fib. tend.* = tendon of flexor fibularis; *fl. hall. br. i. h.* = tibial head of flexor hallucis brevis; *fl. tib. tendon* = tendon of flexor tibialis; *j. tend.* = vincula; *l. fl. tend.* = long flexor tendon; *lumbs.* = lumbricals. X approx. $\frac{1}{2}$ natural size.

specimen studied, it can nevertheless be accurately identified by its course along the ankle and in the sole of the foot. It enters the foot on its tibial side under cover of the lacinate ligament, its tendon lying just posterior to that of the *tibialis posterior*. In the sole the tendon of the

tendons of the various toes. The *flexor tibialis* supplies nearly all of the tendon of the long flexor of the hallux from its dorsal surface, nearly all of the perforating tendon for the second toe, the minor portion of the perforating tendon of the third toe, and only a small portion of the per-

forating tendon of the fourth toe. As I have already stated, the deep head of the *flexor digitorum brevis* arises from the plantar surface of the long tibial flexor.

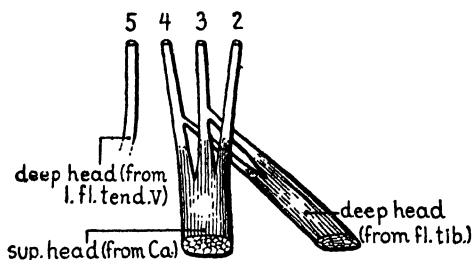


FIG. 5. GORILLA BERINGEI (No. 47). DIAGRAM TO SHOW DISTRIBUTION OF THE HEADS OF THE FLEXOR DIGITORUM BREVIS

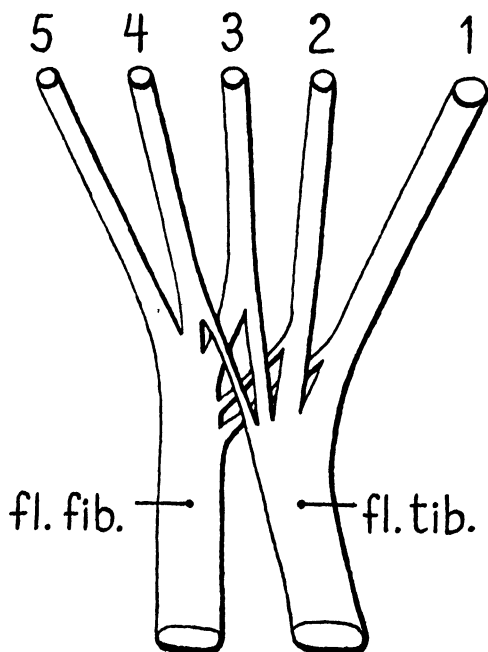


FIG. 6. GORILLA BERINGEI (No. 47). DIAGRAM TO SHOW DISTRIBUTION OF THE LONG FLEXOR TENDONS
fl. fib. = flexor fibularis; fl. tib. = flexor tibialis

M. flexor fibularis (= *M. flexor hallucis longus*) (figs. 2, 4, 6, 7, 15). Like that of the flexor tibialis, the origin of this muscle is lacking. Its identity can likewise be established by its position in ankle and

foot. The rounded tendon goes along the *sulcus M. flexoris hallucis longi* of the talus and calcaneus, under cover of the lacinate ligament, posterior to the tendon of the *flexor tibialis*, over the plantar surface of the *sustentaculum tali*, and along the sole of the foot to join the tendon of the tibial flexor. At the point of junction the tendon of the fibular flexor is dorsal to that of the other long flexor. The *flexor fibularis* contributes a small portion of the long hallucal flexor tendon, sends a minor contribution to the perforating tendon of

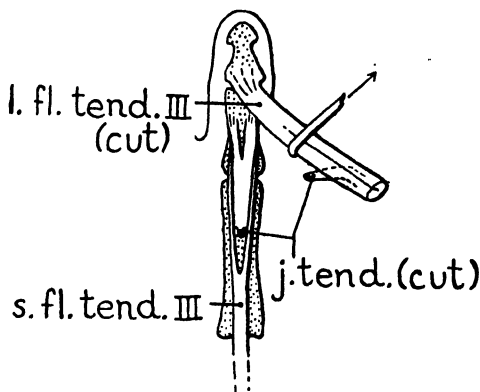


FIG. 7. GORILLA BERINGEI (No. 47). MODE OF INSERTION OF FLEXOR TENDONS

j. tend. = vincula; l. fl. tend. = long flexor tendon; s. fl. tend. = short flexor tendon. X approx. $\frac{1}{2}$ natural size.

the second toe, and supplies the major portions of the perforating tendons of the third and fourth toes, and all of the long flexor tendon of the fifth toe. The long flexor tendons for the four lateral toes (after perforating the short flexor tendons of their respective digits) are inserted into the bases of the terminal phalanges. There is no perforated (short flexor) tendon for the fifth toe, but the terminal long flexor tendon for that digit gives off, from its dorsal aspect, a very definite tendon which inserts into the middle phalanx of toe V as do the perforated tendons of the

other toes. This accessory tendon seems undoubtedly to represent the short flexor tendon of V which has become attached to the long flexor tendon of that toe. The course of the long flexor tendon of the great toe lies, as in man, between the heads of the *flexor hallucis brevis* and it inserts into the base of the terminal phalanx.

Source of long flexor tendons:

Flexor fibularis (1) (2) 3 4 5.

Flexor tibialis 1 2 (3) (4).

M. quadratus plantae. This muscle is absent.

Mm. lumbricales (fig. 4). These are four in number, spindle-shaped, very large and powerful, arising from the long flexor tendons in the sole. The innermost (for second toe) arises by a single head from the tibial side of the long flexor tendon for II. Those for the third, fourth and fifth toes arise by two heads, from the adjacent sides of the long flexor tendons. That for III therefore takes origin from the fibular side of the tendon for II and the tibial side of the tendon for III; that for IV from the fibular side of the tendon for III and the tibial side of the tendon for IV; and that for V from the fibular side of the tendon for IV and the tibial side of the tendon for V. The insertions are somewhat into the tibial sides of the basal phalanges of the four outer toes, with very definite extensions (narrow tendons) into the extensor aponeuroses. *Innervation:* the *lumbricales* for toes II, III and IV receive branches from the medial plantar nerve, that for toe V from the superficial ramus of the lateral plantar nerve.

M. tibialis posterior (figs. 8, 15). The tendon lies anterior to that of the *flexor tibialis*, and posterior to those of the *tibialis anterior*. It passes under cover of the lacinate ligament and inserts by a broad, flat tendon on the medial and plantar surfaces of the tuberosity of the

naviculare, is prolonged to the plantar surfaces of the cuneiforms, and also sends fibres to the *sustentaculum tali* and sheath of the *peroneus longus*.

M. flexor hallucis brevis (figs. 2, 4, 9, 10). This is a large and well-developed muscle. The tibial head arises from the sheath of the *peroneus longus*, *cuneiforme I* and the *naviculare*. The muscle-fibres are attached on either side of the tendon of the *abductor hallucis*, and insert in common with this

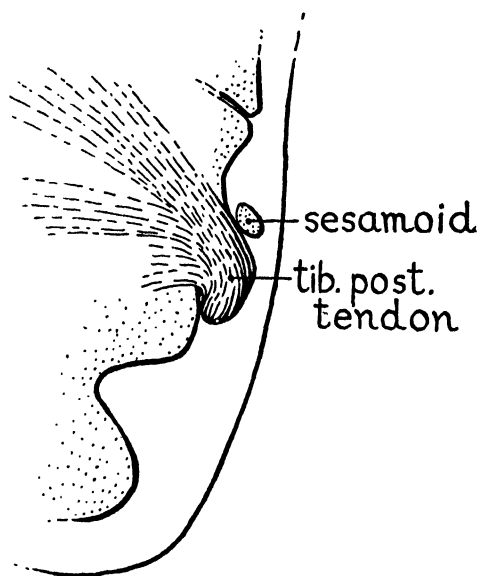


FIG. 8. GORILLA BERINGEI (No. 47). ARRANGEMENT OF TENDON OF TIBIALIS POSTERIOR ON PLANTAR SURFACE OF FOOT

× $\frac{1}{3}$ natural size

into the tibial side of the base of the basal phalanx of the hallux and also into the metatarso-phalangeal joint capsule of the great toe. A few muscle fibres from the inner head are also inserted into the neck of the shaft of the first metatarsal bone, thus forming a rudimentary and quite feeble *opponens hallucis* (fig. 9). The fibular head of the *flexor hallucis brevis* is not a distinct muscle, but is united with the oblique portion of the *adductor hallucis*.

At first glance these two muscles appeared to be completely fused, so that I first obtained the impression that the fibular head of the *flexor hallucis* was absent, and that the *adductor hallucis obliquus* received a double nerve-supply, from each of the plantar nerves. Further investigation proved plainly that this was not the case. The inner (tibial) portion of this compound muscle, the portion which received the nerve from the *N. plantaris medialis*, was easily separated on its plantar surface

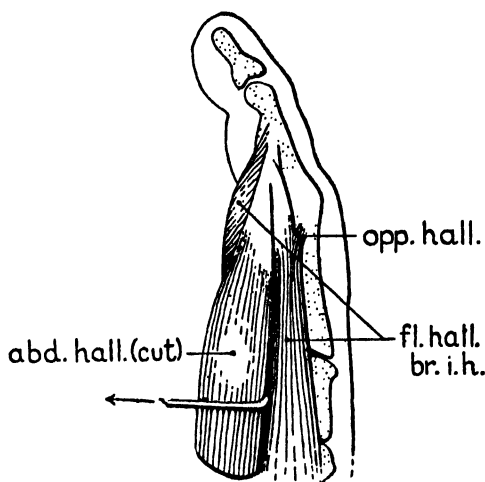


FIG. 9. GORILLA BERINGEI (No. 47). MEDIAL VIEW OF GREAT TOE

abd. hall. = abductor hallucis; *fl. hall. br. i. h.* = tibial head of flexor hallucis brevis; *opp. hall.* = opponens hallucis. X approx. $\frac{2}{3}$ natural size.

from the rest of the muscle, which was found to be innervated by the *N. plantaris lateralis*. A strong sheet of muscle, extending from the proximal end of the flexor to the distal end of the adductor element, unites the two muscles. On the dorsal surface, no natural separation of the compound muscle into its flexor and adductor components is to be found. I am therefore disposed to consider the tibial element, arising from the first and second cuneiform bones and sheath of the *peroneus longus*, and supplied by the medial

plantar nerve, as representing the fibular head of the *flexor hallucis*; the fibular portion, which takes origin from the bases and proximal parts of the shafts of the third and second metatarsals, the interosseous fascia, and sheath of the *peroneus longus*, and which receives branches of the lateral plantar nerve, must then be the true oblique head of the *adductor hallucis*. It seems more logical to regard this doubly-innervated muscle mass in this manner, rather than simply as an *adductor obliquus* with dual nerve supply, especially since the usual fibular head of the *flexor hallucis brevis* is not otherwise represented. But because of the complete dorsal fusion and the occurrence of the plantar connecting muscle-sheet, it is of course impossible to say just where one muscle ends and the other begins. The tibial head of the *flexor hallucis brevis* is larger than the muscle-mass which represents the fibular head. *Innervation*: the tibial head of the *flexor brevis* is supplied by branches of the medial plantar nerve; the fibular head, as already stated, receives its nerve-supply from the same nerve.

M. adductor hallucis (*M. contrabens I*) (figs. 10, 11). This is a large and powerful muscle. It is clearly divided into transverse and oblique heads. The transverse head (*M. transversalis pedis* of older authors) arises from the proximal parts of the heads and most distal parts of the shafts of the fourth, third and second metatarsals, from the joint-capsules and transverse metatarsal (capitular) ligaments of these bones, from the fascia over the intervening interosseous muscles, and also slightly from the deep slips of the fibular portion of the plantar aponeurosis. The oblique head arises from the bases of the third and second metatarsals, from the fascia over the intervening interosseous muscles, from the sheath of the *peroneus longus* and *cuneiformia I* and *II*. This

oblique head contains the fibular head of the *flexor hallucis brevis* (see previous section dealing with the latter muscle). The transverse head inserts fleshily into the fibular side of the base of the basal phalanx of the hallux, the metatarso-phalangeal joint-capsule of that toe, and dorsally into the head and neck of the shaft of *metatarsale I*. In addition, it gives off muscular slips which insert higher up in the fibular

oblique receives, in addition, a branch from the medial plantar nerve; this nerve supplies the more tibial portion of the muscle, which I regard as representing the fibular head of the *flexor hallucis brevis*, fused with the true *adductor obliquus*.

I have found no certain traces of other elements of the adductor layer of muscles (i.e., *Mm. contrahentes II, IV, V*). There

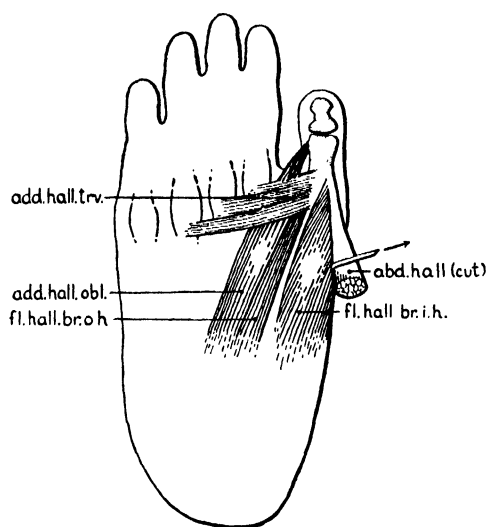


FIG. 10. GORILLA BERINGEI (No. 47). SHORT PLANTAR MUSCLES OF GREAT TOE

abd. hall. = abductor hallucis; *add. hall. obl.* = oblique head of adductor hallucis; *add. hall. trv.* = transverse head of adductor hallucis; *fl. hall. br. i. h.* = tibial head of flexor hallucis brevis; *fl. hall. br. o. h.* = fibular head of flexor hallucis brevis. X approx. $\frac{1}{2}$ natural size.

side of the first phalanx. The insertion on the first metatarsal bone extends for a considerable distance (about 1.5 cm.). The oblique head (including the fibular head of the *flexor hallucis brevis*), inserts fleshily into the hallucal metatarso-phalangeal joint-capsule in common with the fibres of the transverse head. *Innervation*: both the transverse and oblique heads are supplied by branches from the deep ramus of the lateral plantar nerve. The

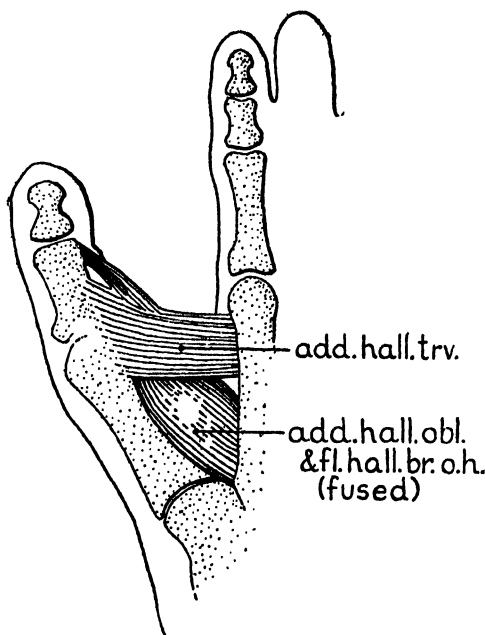


FIG. 11. GORILLA BERINGEI (No. 47). DORSAL VIEW OF ADDUCTOR HALLUCIS

add. hall. obl. = oblique head of adductor hallucis; *add. hall. trv.* = transverse head of adductor hallucis; *fl. hall. br. o. h.* = fibular head of flexor hallucis brevis. X approx. $\frac{1}{2}$ natural size.

was a tough aponeurotic sheet covering the more lateral interosseous muscles on their plantar aspect, but this cannot with any certainty be interpreted as vestiges of the lateral contrahentes. In the orang-utan, Ruge (1878b) and I have found the lateral contrahentes in a vestigial condition, represented by a tough tendon-plate with extensions to the lateral digits. Their identity can be established by the course of

the deep division of the lateral plantar nerve, which separates this tendon-plate and the *adductor hallucis* from the deeper interosseous muscles. Ruge demonstrated that a separation of contrahentes (including of course the contrahens of the hallux, or *adductor hallucis*) and interossei by the deep ramus of the lateral plantar nerve is constant among mammals. Cunningham (1882, p. 136) states, "So far as I am aware this rule fails to apply to the foot in only two cases, viz., the *Dasyurus viverrinus* and *Dasyurus hallucatus*, in both of which the nerve passes under cover of one of the abductors of the minimus." According to Kohlbrugge (1897), in all Primates the deep ramus of the lateral plantar nerve lies under the aponeurosis of the contrahentes and over the interossei. This rule, however, knows exceptions, for among the gibbons Kohlbrugge found that a considerable part of the interossei lay over the deep ramus of the nerve. The rule formulated by Ruge is, nevertheless, of tremendous value, and is our sole guide in determining the identity of the contrahentes when only vestiges are present. In my gorilla, the tendinous sheet covering the lateral interossei had no very definite extensions to the digits such as Ruge and I found in the orang, and no portion of it was over (plantar to) the main trunk of the deep ramus of the lateral plantar nerve. It lay entirely distal to the main trunk of this nerve. I am therefore not at all certain that this sheet should be regarded as constituting degenerated elements of the contrahens layer. It is of course possible to consider this aponeurosis as constituting the distal portion of the degenerated outer part of the layer of contrahentes, and the proximal portion as having entirely disappeared. Such an assumption would explain the position of the nerve in respect to this sheet.

Mm. interossei dorsales et plantares (figs.

12, 13, 14). There are four dorsal and three plantar interosseus muscles. These muscles arise as in man, the dorsal muscles by two heads, the plantar by one. Two of the dorsal set are inserted on the second toe, one on each side of that digit; the remaining members of this series are inserted on the fibular sides of the third and fourth toes. The second dorsal interosseus arises from the sheath of the *peroneus longus*, the base and fibular half of the plantar surface of the shaft of *metatarsale II*, from the fibular side of the shaft and the fibular half of the dorsum of the same bone, with a second head from the tibial side of the shaft and the tibial half of the dorsum of *metatarsale III*. The third and fourth dorsal interossei have similar origins in relation to the third and fourth and to the fourth and fifth metatarsals, respectively. The first dorsal interosseus arises from the sheath of the *peroneus longus*, the base and tibial half of the plantar surface of the shaft of *metatarsale II*, from the tibial side of the shaft and the tibial half of the dorsum of the same bone, with an additional head of origin from the fibular side of the dorsum of the first cuneiform bone. In addition the first dorsal interosseus exhibits a sort of accessory slip, of good size, arising from the plantar surface of *metatarsale II*, from the interval between the main muscle-masses of the first and second dorsal interossei. This slip goes to the tibial side of the basal phalanx of the second toe and joins the main tendon of insertion of *dorsal interosseus I*. It seems undoubtedly to be a detached portion of the first dorsal interosseus (figs 12, 13, 14). The dorsal interossei insert into the sides of the bases of the basal phalanges of their respective digits, and send seemingly slight extensions into the extensor aponeuroses.

The plantar interossei are inserted into the tibial sides of the bases of the basal

phalanges of the third, fourth and fifth toes, with seemingly slight extensions into the extensor aponeuroses. Their origins are similar to those of the dorsal set, although of course limited to a single metatarsal bone. They therefore have but single heads of origin. The first plantar interosseus arises from the sheath of the *peroneus longus*, the base and tibial half of the plantar surface of the shaft of

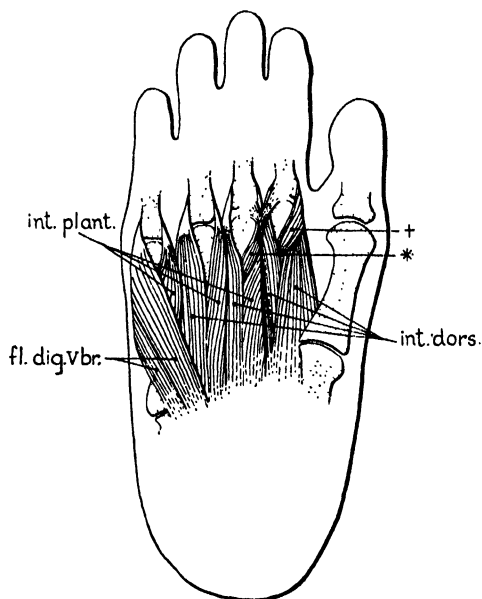


FIG. 12. GORILLA BERINGEI (No. 47). PLANTAR VIEW OF THE INTEROSSEOUS MUSCLES

fl. dig. V br. = flexor digiti V brevis; *int. dors.* = dorsal interossei; *int. plant.* = plantar interossei; + = slip to first dorsal interosseus; * = accessory muscle to second and third toes. X approx. $\frac{1}{3}$ natural size.

metatarsale III, and from the tibial side of the shaft of that bone. The two remaining plantar muscles have similar relations to *metatarsalia IV* and *V*. The interossei arising entirely or in the main from any one metatarsal are not clearly separated in regard to their origins on the proximal part of the plantar surface of the bone, so that each pair of interossei for a single toe arise primarily from a common

plantar muscle-mass. In the case of the third plantar interosseus, this has a common origin with the *flexor digiti V brevis*.

Intimately connected with interossei, there occurs a curious small muscle, which arises from the plantar surface of *metatarsale III*, from the interval between the first plantar and third dorsal muscles, just proximal to the head of the bone. This muscle divides into two parts, which insert into the metatarso-phalangeal joint capsules of the second and third toes,

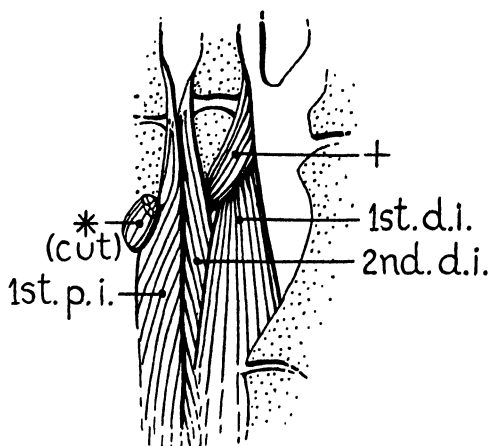


FIG. 13. GORILLA BERINGEI (No. 47). DETAIL TO SHOW RELATION OF ACCESSORY MUSCLE OF SECOND AND THIRD TOES TO THE INTEROSSEI

d. i. = dorsal interosseus; *p. i.* = plantar interosseus. The other symbols are the same as in the previous figure. X approx. $\frac{1}{3}$ natural size.

plantar to the insertions of the interossei (figs. 12, 13). I could find no separate nerve for this muscle, which lies beneath (dorsal to) the deep ramus of the lateral plantar nerve. It is significant that I have found an identical muscle in the foot of the juvenile female gorilla (also *Gorilla beringei*, No. 7), which I have examined; but because all of the superficial muscles and all of the nerves had been removed when first I saw this specimen, I was unable to ascertain its further relations. This muscle is probably a portion of the deepest

plantar layer of muscles, which forms the two sets of interossei and *flexor digiti V brevis* (the *Mm. flexores breves* of some of the more primitive mammals). Its nerve-supply would seem most probably to have been derived from the branch to one of the two interossei with which it is primarily related (first plantar and third

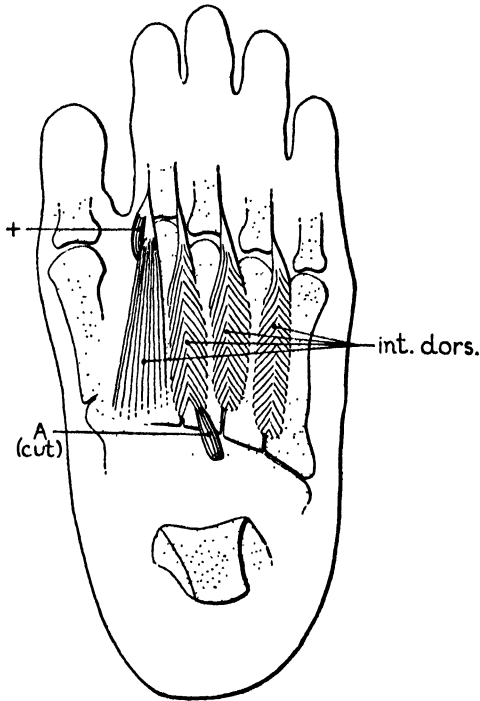


FIG. 14. GORILLA BERINGEI (No. 47). DORSAL VIEW OF THE INTEROSSEOUS MUSCLES

int. dors. = dorsal interossei; + = slip to first dorsal interosseus; A = accessory short extensor belly to second dorsal interosseus. X approx. $\frac{1}{2}$ natural size.

dorsal). Moreover, it seems extremely likely that the muscle is merely a detached slip from the common muscle mass giving rise to these interossei.

The second dorsal interosseus also receives muscle fibres from the short extensor muscles on the back of the foot in the form of a small accessory belly (figs. 14, 17).

The interossei of this gorilla foot are

thus arranged as in the foot of man, so that the dorsal set acts partly as abductors of the toes from an axis running through the mid-line of the second digit, while part of the function of the plantar set is to adduct the toes towards this imaginary axis. A similar arrangement existed in the other specimen of *Gorilla beringei* (No. 7) which I studied. Only the dorsal series can be seen from the dorsum of the foot, while both sets project into the sole. *Innervation*: all of the interossei receive branches of the deep ramus of the lateral plantar nerve which enter the plantar surfaces of the muscles.

M. flexor digiti V brevis (figs. 2, 3, 12). This muscle, from its topographical relations and nerve-supply, belongs to the interosseous series, being the most lateral of that group. It arises in two layers. The superficial layer has origins from the sheath of the *peroneus longus*, cuboid, base of the fifth, and slightly from the base of the fourth metatarsals. This layer lies plantar to the proximal portion of the third plantar interosseus, with whose fibres it blends slightly, and also plantar to the tendon of the *abductor digiti V*. It joins the deep layer on the outer side of the foot. The deep layer arises from the sheath of the *peroneus longus*, the proximal portion of the fibular half of the plantar surface of the shaft and from the base of *metatarsale V*, and from the proximal three-quarters of the fibular side of the shaft and distal portion of the tuberosity of that bone. The tendon of the *abductor digiti V* pierces the muscle in a manner which separates the superficial from the deep portion. The combined layers insert by a rather broad and flat tendon into the fibular side of the basal phalanx of the fifth toe, with a slight extension into the extensor aponeurosis. *Innervation*: from the deep division of the lateral plantar nerve.

M. opponens digiti V. This muscle is absent.

Muscles of the Dorsum of the Foot

M. extensor hallucis longus (figs. 15, 17). The insertion is by a broad flat tendon into the base of the terminal phalanx of the great toe, with a slight expansion at the base of the basal phalanx on each side of the tendon of the *extensor hallucis brevis*.

M. extensor digitorum longus (figs. 15, 17). The main tendon of this muscle divides into three flat tendons. One supplies the fifth toe, another the fourth, while the third re-divides into tendons for the third and second toes. The tendon for the second toe is smaller than the others. All of these tendons expand over the heads of their respective metatarsal bones into broad aponeuroses over the digits.

The extensor aponeurosis on the dorsum of each of the four lateral toes (II-V), which is formed by tendons of the *extensor digitorum longus*, *extensor digitorum brevis* (except in the case of that for toe V), the lumbrical and the two interossei for that toe, inserts as in man,—i.e., by a tendinous expansion to the basal phalanx, by a middle slip to the base of the middle phalanx, and by two lateral slips to the base of the terminal phalanx. I have not been able to trace out completely the various components of the extensor aponeurosis in my gorilla, probably because it had long been preserved. (Willan (1912) states that the distinction between the various tendons and the ensheathing aponeurotic sheet can be most easily demonstrated in fresh specimens.) In addition, these aponeuroses had been considerably injured in the process of skinning.

M. peroneus tertius (fig. 15). This muscle was already laid bare and dissected when I received the foot. The relations when seen by me were as follows:—The tendon inserts into the outer side of the base and proximal portion of the shaft of the fifth

metatarsal bone by a tendinous sheet, inserting as two layers. Its association with the *extensor digitorum longus* is plainly shown by its fascial connections, the tendons of the two muscles being united by a very tough fascia.

M. tibialis anterior (figs. 15, 16). The insertion is by three definite tendons. The

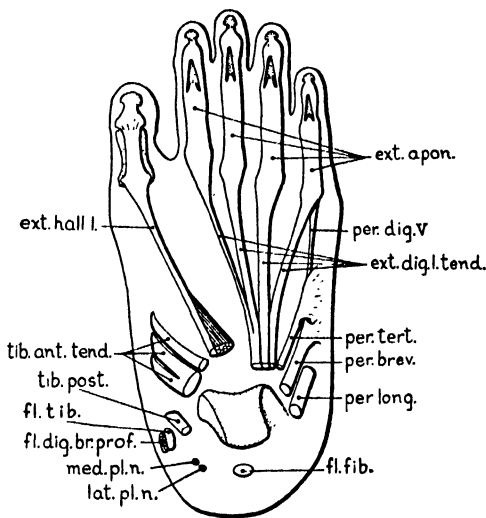


FIG. 15. GORILLA BERINGEI (No. 47). ARRANGEMENT OF THE TENDONS ON THE DORSUM OF THE FOOT

ext. apon. = extensor aponeuroses; *ext. dig. l. tend.* = tendons of extensor digitorum longus; *ext. hall. l.* = extensor hallucis longus; *fl. dig. br. prof.* = deep head of flexor digitorum brevis; *fl. fib.* = tendon of flexor fibularis; *fl. tib.* = tendon of flexor tibialis; *lat. pl. n.* = lateral plantar nerve; *med. pl. n.* = medial plantar nerve; *per. brev.* = tendon of peroneus brevis; *per. dig. V* = vestige of peroneus digiti V; *per. long.* = tendon of peroneus longus; *per. tert.* = tendon of peroneus tertius; *tib. ant. tend.* = tendons of tibialis anterior; *tib. post.* = tendon of tibialis posterior. X approx. $\frac{1}{2}$ natural size.

most anterior tendon curves around the inner border of the foot to insert on the plantar surface of the base of the metatarsal of the hallux. The middle and posterior tendons are at first joined, then split before their insertions. The middle tendon curves around the inner border of the foot and inserts by a broad expansion into the inner surface of the first cuneiform.

The posterior tendon also curves around the inner border and ends on a large sesamoid bone just distal to the tuberosity of the *navicular*.

Mm. extensores hallucis et digitorum breves (figs. 3, 17). These muscles are in reality merely more or less marked divisions of a single muscle, which arises from the lateral and dorsal surfaces of the calcaneus, and also slightly from the under surface of the cruciate ligament. The origin lies close to the part of the *abductor digiti V* which forms the *abductor ossis metatarsi V*, and also close to the tendon of the *peroneus brevis*. The muscle divides into four more or less distinct bellies. That for the hal-

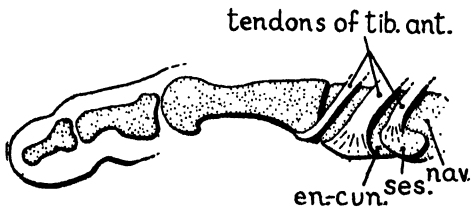


FIG. 16. GORILLA BERINGEI (No. 47). MEDIAL VIEW OF FOOT, TO SHOW INSERTIONS OF TENDONS OF TIBIALIS ANTERIOR

tib. ant. = tibialis anterior; *en-cun.* = cuneiform I; *nav.* = navicular; *ses.* = para-navicular sesamoid. X approx. $\frac{2}{3}$ natural size.

lux is quite distinct because of its oblique course towards the great toe; it forms the part commonly known as the *M. extensor hallucis brevis*, which inserts into the basal phalanx of the hallux by a broad tendinous expansion. The remaining bellies insert into the fibular sides of the extensor aponeuroses of the tendons of the *extensor digitorum longus*, and form parts of these aponeuroses for the second, third and fourth toes. There is no short extensor tendon for the fifth toe. An additional muscle-belly, already mentioned in connection with the dorsal interossei, arises as a continuation of that portion of the muscle which forms the bellies for the first and second toes, but chiefly from the

former. This little muscle is prolonged into the second dorsal interosseus, its fibers being continuous with those of the latter (figs. 14, 17). *Innervation*: the *extensores hallucis et digitorum breves* receive branches of the deep peroneal nerve. There is no separate nerve for the accessory muscle-belly running to the *dorsal interossei II*; perhaps it receives its fibres from one of

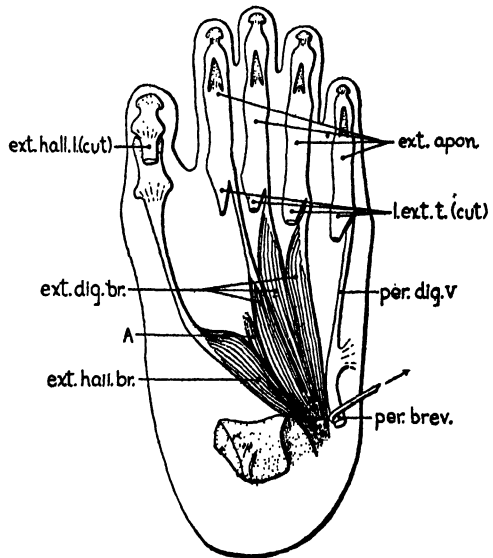


FIG. 17. GORILLA BERINGEI (No. 47). DORSUM OF FOOT TO SHOW SHORT EXTENSOR MUSCLES

ext. apon. = extensor aponeuroses; *ext. dig. br.* = extensor digitorum brevis; *ext. hall. br.* = extensor hallucis brevis; *l. ext. t.* = tendons of extensor digitorum longus; *per. brev.* = tendon of peroneus brevis; *per. dig. V* = vestige of peroneus digiti V; *A* = accessory short extensor belly to second dorsal interosseus. X approx. $\frac{2}{3}$ natural size.

the other branches, in the substance of the muscle itself.

M. peroneus longus (figs. 15, 18). This is represented by a thick, rounded tendon, about twice the diameter of that of the *peroneus brevis*, and lying posterior to the latter. It reaches the plantar surface of the foot by descending just medial to the *abductor ossis metatarsi V*. Covered by a strong sheath it reaches the tibial side of the foot and inserts by a flattened tendon

into the fibular plantar surface of the base of the metatarsal of the great toe. In addition, during its course across the sole, it gives off a definite, narrow tendon to the outer dorsal surface of the cuboid, and the portion of the tendon lying in the peroneal sulcus of the cuboid is attached to this bone by a tough, tendinous plate. There is no sesamoid bone in the portion

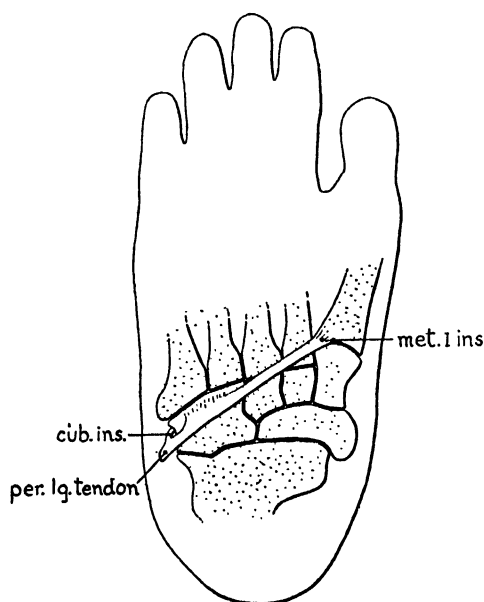


FIG. 18. GORILLA BERINGEI (No. 47). PLANTAR VIEW SHOWING TENDON OF PERONEUS LONGUS

cub. ins. = insertion of peroneus longus on cuboid;
met. I ins. = insertion of peroneus longus on metatarsal I; *per. lg. tendon* = tendon of peroneus longus.
 X approx. $\frac{1}{3}$ natural size.

of the tendon lying over the outer side of the cuboid.

M. peroneus brevis (figs. 15, 17). The tendon of this muscle lies, in the ankle, anterior to that of the *peroneus longus*. The thick, rounded tendon flattens out at its insertion into the dorsal and outer sides of the tuberosity of the fifth metatarsal bone. In addition, the main tendon gives off, just prior to its insertion, a narrow, flat tendon which runs between the two

layers of the insertion of the *peroneus tertius* and passes forward along the dorsum of *metatarsale V* to join the extensor tendon to digit V on its deeper surface (figs. 15, 17). This little tendon represents the vestiges of a *M. peroneus digiti V*.

Sesamoid bones. X-ray photographs of the foot, kindly taken by my colleague, Dr. E. C. Hill, show that there are no sesamoids, other than the one already mentioned in connection with the insertion of the *tibialis anterior*. These plates also show that all of the epiphysal lines are completely obliterated.

NERVES OF THE FOOT

The nerves of the foot require but little mention, for their distributions follow the usual course found in man. As previously stated, the skinned condition of the foot has prevented me from studying the cutaneous distribution.

Nerves of the Sole of the Foot

At the point where the foot has been severed from the leg, the two plantar nerves are already separate entities. They here lie posterior and internal to the *flexor tibialis* (fig. 15). The lateral plantar nerve is the more posterior and lies slightly external to the medial plantar nerve. Both nerves reach the sole under cover of the lacinate ligament.

Medial plantar nerve (fig. 19). Its course is along the inner border of the foot. Branches are first given off for the superficial head of the *flexor digitorum brevis* and *abductor hallucis*. Distal to these it divides into two main trunks, the medial of which innervates the tibial head of the *flexor hallucis brevis* and ends in a cutaneous branch near the tip of the hallux; the lateral trunk supplies branches to the fibular head of the *flexor hallucis brevis* (which is united to the *adductor hallucis obliquus*), the *lumbricales* of toes II, III and IV, and ends in

cutaneous branches over the base of the second toe and in the first interosseous space.

Lateral plantar nerve (fig. 19). From the point where it enters the planta on the inner border it curves over sharply toward

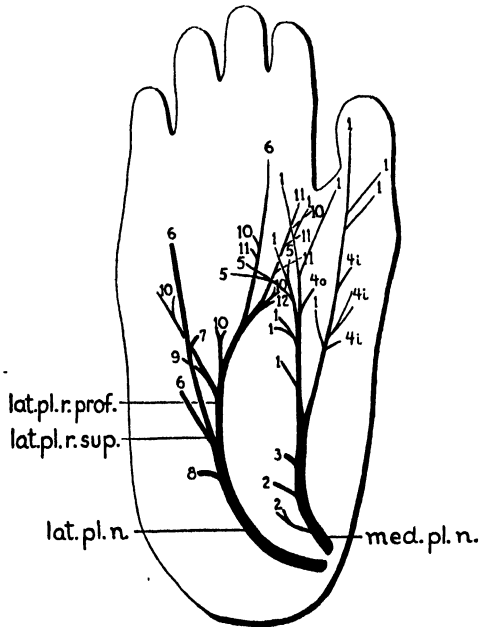


FIG. 19. GORILLA *BERINGEI* (No. 47). NERVES OF THE SOLE

med. pl. n. = main trunk of medial plantar nerve; *lat. pl. n.* = main trunk of lateral plantar nerve; *lat. pl. r. prof.* = deep division of lateral plantar nerve; *lat. pl. r. sup.* = superficial division of lateral plantar nerve; 1 = cutaneous branches of medial plantar nerve; 2 = to superficial head of flexor digitorum brevis; 3 = to abductor hallucis; 4i = to tibial head of flexor hallucis brevis; 4o = to fibular head of flexor hallucis brevis; 5 = to lumbricals of toes II, III and IV; 6 = cutaneous branches of lateral plantar nerve; 7 = to lumbrical of toe V; 8 = to abductor digiti V; 9 = to flexor digiti V brevis; 10 = to interosseous muscles; 11 = to adductor hallucis transversus; 12 = to adductor hallucis obliquus. X approx. $\frac{1}{4}$ natural size.

the lateral side of the foot. From its main trunk it supplies the *abductor digiti V*, and then splits into its superficial and deep divisions. The superficial division is sensory except for a branch which innervates the lumbrical of toe V. The deep division curves inwards and deep, and lies between

the *adductor hallucis* and the interosseous muscles. It innervates the *flexor digiti V brevis*, both heads of the *adductor hallucis*, and all of the interossei (both plantar and dorsal), and also gives off sensory branches. There was no anastomosis between the plantar nerves.

Nerves of the Dorsum of the Foot

Deep peroneal nerve (fig. 20). It runs beneath the short extensor muscles and divides into two parts. One division goes as a cutaneous nerve to the first interdigital space, while the other division innervates the short extensors of the hallux and toes II-IV and also gives off a sensory branch.

I also wish to note that none of the dorsal interossei received any visible nerve-supply from the deep peroneal nerve, despite the accessory fibres from the short extensor to *dorsal interosseus II*.

COMPARISON WITH THE LOWLAND GORILLA (*G. GORILLA*) AND OTHER PRIMATES

In the succeeding comparisons, my specimens will be referred to by their respective collection numbers, thus: No. 47 = the adult female *Gorilla beringei* of which I have just given a detailed description; No. 7 = the juvenile female *G. beringei* in which I studied the interosseous muscles; No. 1105 = the infant female *G. gorilla* dissected by Dr. Morton, and on which I have made certain observations; and No. 5 = the infant female *G. gorilla* in which I noted the arrangement of the interosseous muscles.

Two important publications (Keith, 1899; Duckworth, 1915), in both of which the foot musculature of the lowland gorilla has been considered, are, unfortunately, of little use to me in the present study. Keith's paper gives some very interesting data on the variability of certain of the foot muscles, which are based upon accounts in the literature, and perhaps also

upon dissections of his own. He gives no bibliography, however, and since there is no way of determining his sources of information (most of which are undoubtedly also considered by me), I am therefore unable to make use of his data in the present more or less statistical study. For

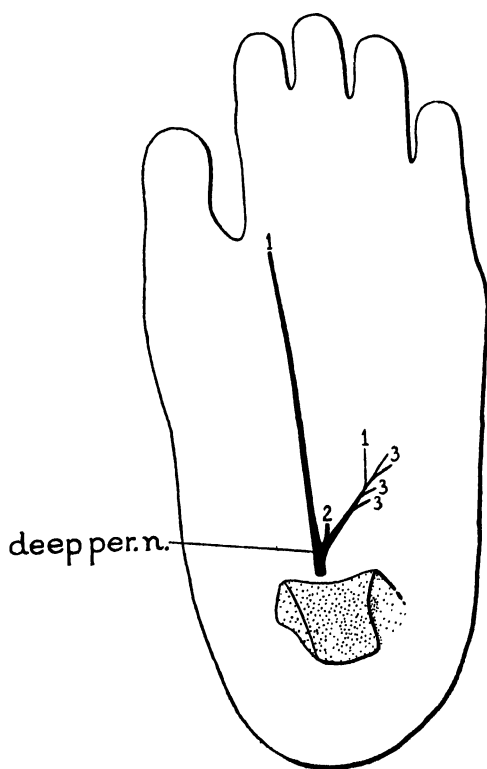


FIG. 20. GORILLA BERINGEI (No. 47). DEEP PERO-NEAL NERVE ON DORSUM OF THE FOOT

deep per. n. = deep peroneal nerve; 1 = cutaneous branches; 2 = to extensor hallucis brevis; 3 = to bellies of extensor digitorum brevis. X approx. $\frac{1}{2}$ natural size.

the same reason I am unable to include the information given by Duckworth. This obviously contains much original work, based upon dissections in the Cambridge University collection, but the author fails to discriminate completely between his own observations and those taken from the literature.

I have been unable to locate a copy of the important paper by Rothschuh (1888), so that my references to his studies on the muscles of the gorilla are cited from the papers of Sommer (1906) and Weidenreich (1922), chiefly from the former source. Likewise, both of the copies of the work of Eisler (1890) which were accessible to me were incomplete, and lacked the pages dealing with the nerves of the foot; my references to this paper have been taken from Kohlbrugge (1897).

The succeeding discussion is entirely limited to Primates. For a discussion of the complete foot musculature in all the groups of Tetrapods, the reader is referred to Ribbing (1909). McMurrich deals with the crural flexors (1904) and plantar muscles (1907) of Tetrapods. The papers of Glaesmer (1908 and 1910) cover the flexor musculature in mammals. Eisler's (1895a) important monograph is also most suggestive and of great interest. These are, naturally, only a few of the more important papers.

For the sake of uniformity, the Primate nomenclature followed in this paper is that of Elliot (1913). This, although not entirely satisfactory, is the best at the present time. When referring to a particular specimen, the author's terminology, if differing from that of Elliot, is given in parentheses. If succeeding reference is made to this specimen, only Elliot's terminology is given. Difficulties were, however, sometimes encountered in synonymizing the names used by certain authors with those given by Elliot. For example, Kohlbrugge (1897) uses the name "*Semnopithecus*" as a collective term for his specimens of *Semnopithecus pyrrhus*, *S. maurus* and *S. nasicus*. These I have identified respectively as *Pygathrix aurata*, *P. cristata* and *Nasalis larvatus*. Elliot does not recognize the genus "*Semnopithecus*," and the sub-family "*Semnopithecinae*" he

terms "*Colobinae*." Since the three forms just mentioned are all included in the "*Colobinae*," I have substituted that name for Kohlbrugge's "*Semnopithecini*." It might also be mentioned that both *Semnopithecus pyrrhus* and *S. maurus* can be identified as *Pygathrix aurata*, but in order to avoid confusion I have called the latter *Pygathrix cristata*, for which it is also a synonym. There is, however, a strong possibility that both *Semnopithecus pyrrhus* and *S. maurus* are actually only varieties of a single species.

Aponeurosis plantaris. The only *aponeurosis plantaris* of a lowland gorilla for comparison with my highland gorilla is that of the young specimen described and figured by Loth (1908). In his animal apparently neither the metatarsal portion of the fibular part of the aponeurosis (*fasciculus fibularis*) nor the slip to the hallux (*fasciculus digiti I*) were as well-developed as in my animal. In other respects, however, the aponeuroses seem to have the same general arrangement. The differences in the fibular and hallucal parts of the structure might, at first glance, appear to constitute a difference between the highland and lowland types of gorilla. But Loth's work demonstrates that the exact form and development of the *aponeurosis plantaris* within a single genus of Primates is quite variable. This variability within a genus may or may not be connected with specific differences. At any rate, it indicates that any conclusions as to differences in the *aponeurosis plantaris* of such closely related forms as *Gorilla gorilla* and *G. beringei*, when based on such meagre material as that which is at present under consideration, mean very little, if anything. The strong development of the aponeurosis in my *G. beringei* strongly indicates an adaptation to a plantigrade mode of locomotion.

The *aponeurosis plantaris* sometimes (e.g.,

in *Galago*) occurs as merely a continuation of the tendon of the plantaris muscle over the *tuber calcanei* into the sole. The plantaris itself may be absent, as it usually is in the anthropoid apes (Kohlbrugge, 1897), and also occasionally in man, yet the aponeurosis always remains as a definite structure. For a most thorough account of the *aponeurosis plantaris* in the various genera of Primates, the reader is referred to the paper of Loth (1908).

M. abductor hallucis. This muscle seems not to be strikingly variable in the known specimens of *G. gorilla*. Its general arrangement quite agrees with that in my *G. beringei*. It arises from the plantar and medial surfaces of the *tuber calcanei*, lacinate ligament, and along the medial border of the foot to the *naviculare* (Hepburn, Pira); from the calcaneal process and calcaneo-scaphoid ligament (Duvernoy); or by two heads, from the calcaneus and from the plantar aponeurosis (Deniker: fetus and juvenile). Macalister states that it arises by two heads. This muscle in the highland gorilla (No. 47) shows a tendency towards two heads, in that it is strongly attached to the plantar aponeurosis in addition to its calcaneal and ligamentous origins. All specimens have the same general insertion into the basal phalanx of the hallux. A connection of the end tendon with the inner head of the *flexor hallucis brevis*, found in No. 47, is also mentioned by Duvernoy, Hepburn, and Pira.

The structure of the muscle is essentially similar in other Primates. In prosimians, e.g., in *Lemur* (Cunningham), *Lemur catta* (Murie and Mivart), and *Daubentonia* (*Chiromys*) *madagascariensis* (Zuckerlandl), it arises only from the plantar aponeurosis, and therefore has no bony origin.

M. abductor digiti V. This muscle is rather uniform in all gorillas, except that

in some its lateral fibres form an *abductor ossis metatarsi V*, which will be discussed below. The origins and insertions, when given, agree in general with the conditions in No. 47. Only Pira describes a partial origin from the fibular portion of the plantar aponeurosis; I found such an origin in No. 47. It may be united with the *flexor digiti V brevis* (Pira, Sommer). No author mentions the condition found in No. 47 where the tendon of the *abductor digiti V* pierces the muscle-belly of the *flexor digiti V brevis*. A partial origin of the abductors of the hallux and minimus from the plantar aponeurosis in monkeys demonstrates the original connection of these muscles with the plantaris tendon (Ribbing). It has a partial origin from the plantar aponeurosis in man. The muscle shows no noteworthy differences in other Primates. It has a calcaneal origin in prosimians (Murie and Mivart, Wool-lard, Zuckerkandl).

M. abductor ossis metatarsi V. This is clearly a derivative of the *abductor digiti V*, with which it is usually united (Hepburn, Sommer, No. 1105, No. 47), but it may be a separate muscle (Pira). In Hepburn's animal there was apparently no separation of the muscle-belly of the *abductor digiti V* to form an *abductor ossis metatarsi V*, but only of the tendon, while in the specimen of Sommer and in Nos. 1105 and 47 the division extended into the muscle-mass itself. Bischoff, Deniker (2 specimens), Duvernoy, Hartmann and Macalister all state the *abductor digiti V* as being present in their gorillas, but none of these writers mention or picture any structure resembling an *abductor ossis metatarsi V*. I therefore feel justified in concluding that it was absent in their animals. An abductor of the fifth metatarsal therefore occurs in the single highland gorilla and in three of nine lowland gorillas (33.3 per cent). If the figures are united the fre-

quency in gorillas is four out of ten (40 per cent). This muscle occurs in man in over 40 per cent of cases (Bryce). It may be a separate structure or a part of the abductor.

This muscle is often found in the chimpanzee (Kohlbrugge), and it was present in my specimen. It is, however, apparently rare in the orang (Le Double cites its presence in one specimen, but it was absent in my animal and in Hepburn's, while neither Kohlbrugge nor Sonntag note its occurrence). I find no reference to it in the gibbons, but it probably occurs at least occasionally in these animals. The abductor of the fifth metatarsal is present in some Old World monkeys, e.g., in my *Pygathrix germaini*, in Cunningham's *Papio papio* (*Cynocephalus sphinx*), and in the bonnet macaque (*Pithecius sinicus*), *Papio cynocephalus* (*Cynocephalus anubis*) and *Papio papio* (*Cynocephalus sphinx*) (Le Double). I have at hand no reference to it in New World monkeys, but it undoubtedly must exist in representatives of this group (Cunningham notes its absence in *Ateles* (?)). The muscle is frequent in prosimians, e.g. in my galago, in *Lemur catta*, *L. nigrifrons*, *Galago crassicaudatus* and *G. garnetti* (Murie and Mivart), in *Lemur* (Cunningham), in *Lemur variegatus* (*varius*) and *Galago* (*Otolicnus*) *crassicaudatus* (Zuckerkandl), in *Daubentonia* (*Chiromys*) *madagascariensis* (Oudemans), and in *Tarsius* (Woollard).

M. flexor digitorum brevis (fig. 21). In all gorillas (except those of Hepburn and Chapman) this muscle is composed of two heads: a superficial, arising from the calcaneus and plantar aponeurosis (Pira, Roths Schuh, Sawalischin, Sommer, No. 47), or from the calcaneus alone (Bischoff, Deniker, Duvernoy, Huxley, Owen), and a deep head, arising on the plantar surface of the tendon of the *flexor tibialis* (Bischoff, Deniker, Duvernoy, Hartmann, Huxley, Owen, Pira, Roths Schuh, Sawalischin,

Sommer, No. 47). In Hepburn's specimen there was only one head, arising chiefly from the calcaneus. Chapman's gorilla had really three distinct heads of origin, namely, a superficial, from the calcaneus, and two deep ones attached respectively to the tendons of the tibial and fibular flexors; the short flexor tendon for toe IV came from the tibial flexor, that for toe V from the fibular. The deep head would

TABLE 1

Sources of the short flexor (*flexor digitorum brevis*) tendons in gorillas. The superficial head in all instances arose from the calcaneus or from that bone and the plantar aponeurosis, the deep head always from the undivided *flexor tibialis* tendon, except in Chapman's specimen, in which the fifth toe tendon arose from that of the *flexor fibularis*

AUTHOR	SUPER- FICIAL HEAD	DEEP HEAD
Bischoff.....	2 3	4 5
Chapman.....	2 3	4 5
Deniker (fetus).....	1 2 3	4
Deniker (juvenile).....	2 3	4 5
Duvernoy.....	2 3	4 5
Hartmann.....	2 3	4 5
Hepburn.....	2 3 4	
Huxley.....	2 3	4 5
Owen.....	2 3	4
Pira.....	2 3	4 5
Rothschuh.....	2 3	3 4
Sawalischin (a).....	2 3	(3) 4
Sawalischin (b).....	2 3	(3) 4 5
Sommer.....	2 3	4 5
No. 47.....	2 3 4	3 (4) 5

seem usually to be fleshy, occasionally a simple tendinous prolongation of the long flexor tendon, but not all writers make this point clear. In Table 1 I have arranged the findings of the various investigators to indicate the sources of origin of the tendons of the *flexor digitorum brevis* for the various toes. This table shows that in the lowland gorilla the tendons for the second and third digits usually arise entirely from the superficial head of

the muscle, in a few cases that for the third may come partially from the deep head. The tendon for the fourth toe nearly always originates solely from the deeper layer, but in one animal wholly from the superficial. The tendon for the fifth digit, when present, is always a product of the deep head. In the single highland gorilla (No. 47) the condition is not exactly similar to that of any of the lowland gorillas, but it falls between the majority, in which the superficial layer supplies only the second and third toes, and Hepburn's specimen, in which all of the tendons arise from the superficial head alone, the deep head being absent. In Hepburn's animal the arrangement agrees with usual conditions in man.

I have found the following arrangements of the *flexor digitorum brevis* in other animals. Chimpanzee: superficial head supplies the tendon for toe II and about half of that for III, the rest of the latter tendon and all of those for IV and V coming from the deep head. Orang: superficial head produces the tendon for II, about half of that for III, and the minor portion of that for IV, the remainder of the tendons for III and IV, and all of that for V, arising from the deep head. *Pygathrix germaini*: the tendon for II arises from the superficial head, those for III, IV and V from the deep. *Galago*: as in *Pygathrix*. In the chimpanzee and orang the superficial head arose from the calcaneus and partly from the plantar aponeurosis, in *Pygathrix* and *Galago* only from the aponeurosis. In all cases the deep head was associated with the undivided tendon of the *flexor tibialis*, and in *Pygathrix* also slightly with that of the *flexor fibularis*.

The tendon to the fifth toe, as already mentioned, is not always present. In addition to the cases listed above, Macalister noted its absence in his gorilla, and I found none in No. 1105. The short flexor

tendon to the fifth toe is therefore completely lacking in seven out of sixteen lowland gorillas. If we combine these cases with the single highland gorilla, in which it was vestigial, we find it lacking in 41.2 per cent of gorillas (seven out of seventeen). My gorilla, No. 47, shows a condition which may be interpreted as representing the short flexor tendon for toe V in the last stages of reduction. As already stated in the description of the *flexor fibularis* of No. 47, the terminal long flexor tendon for toe V gives off a tendinous slip which inserts on middle phalanx V in the manner of a short flexor tendon. Apparently this same tendon in Duvernoy's gorilla, judging from his description and illustration (plate X), was in a state of reduction similar to that exhibited by No. 47. Schwalbe and Pfitzner (1894) found the tendon to the little toe to be absent in Europeans of both sexes in 25 per cent (135 out of 540) of all feet examined. This tendon was absent in 24.4 per cent (161 out of 659) of Japanese feet (Adachi, 1910) and in 18.4 per cent (21 out of 114) of Negro feet (Loth, 1912).

Judging from accounts in the literature, this fifth toe tendon is not so frequently lacking in the chimpanzee, orang and gibbon as it is in the gorilla. Kohlbrugge's table shows it to have been absent in four out of thirteen chimpanzees (30.8 per cent); in three out of fourteen orangs (21.4 per cent); in three out of eight gibbons (37.5 per cent). I found it in both my chimpanzee and orang. Its absence in other Primates would seem to be a very rare occurrence. Sawalischin found it in all of her monkeys and prosimians. It was present in my *Pygathrix* and *Galago*. But Rothschild found it absent in two baboons. It may be concluded that in the reduction of the *flexor digitorum* tendon to the fifth toe the gorilla, chimpanzee and gibbon have progressed

further than has man, and the orang about as far. Of added significance is the fact that this reduction is practically confined to the anthropoids and man.

The fifth toe tendon may be imperforate in the gorilla (Chapman, Huxley). The vestigial tendons for this digit found in Duvernoy's animal and No. 47 were likewise not perforated. Lack of perforation of this tendon may also occur in other anthropoids (Kohlbrugge) and in man (Bryce).

An accessory flexor of the hallux, arising from the inside of the calcaneus between the origins of the *flexor digitorum brevis* and the *abductor hallucis*, and inserting by a long tendon into the basal phalanx of the great toe, was found by Deniker in his fetal gorilla. He homologizes this muscle, after its mode of termination, with the perforated tendons of the other toes. A similar muscle has been noted in the orang by Barnard (1875) and in *Tarsius* by Allen (1898). The "*fasciculus hallucis*" found by Sawalischin in *Pithecius irus* (*Macacus cynomolgus*) and *Lasiopyga* (*Cercopithecus callitrichus*), and the "*flexor brevis hallucis superficialis*" of *Tarsius* (Burmeister, Woolard) would also seem to be homologous structures.

In order to understand the condition of the *flexor digitorum brevis* in the gorilla, it is necessary to survey briefly the morphology of this muscle. The researches of Ribbing (1909) indicate that the entire *flexor digitorum brevis* of mammals (i.e., both heads) should be regarded as a part of the outer flexor mass of the leg, and as representing the more superficial part of the *flexores breves superficiales* of amphibians and reptiles. It is not necessary to go into a lengthy discussion concerning its probable original condition in Tetrapods, i.e., whether it primarily consisted of a single superficial head or a single deep head, or was already divided into superficial and

deep layers. At least it is quite clear, from the investigations of Sawalischin and others, that within the order Primates there is a distinct tendency for the muscle to present a single superficial origin, and for the deep head to become eliminated. Whether the deep head has actually disappeared, or whether it has become united with the superficial head, or otherwise modified, are points which need not long detain us here (on these points see Weidenreich, 1922, S. 241-250). The available evidence indicates that, among the Primates at least, an actual transfer of the deep head from long flexor tendon to cal-

of course excepted) supplied solely from the deep head of the muscle (attached to the tendon of the *flexor tibialis* or to both long flexor tendons). There is also a tendency for the tendons for III and IV to arise in whole or part from the superficial head in a few prosimians and monkeys (Sawalischin). The condition in the gibbons is practically the same as in most monkeys and prosimians, in that nearly all specimens exhibit the superficial head supplying only the second toe (Glaesmer, Kohlbrugge, Sawalischin). In the three great apes, however, there is a much closer approach to the human condition, the ten-

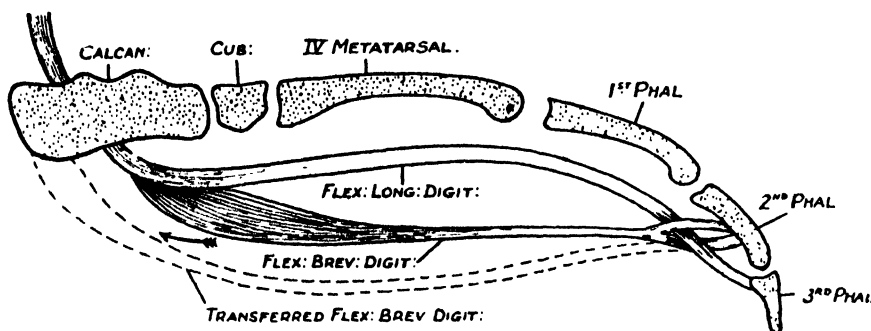


FIG. 21. SECTION OF THE FOOT OF A MONKEY THROUGH THE TARSA AND FOURTH DIGIT, TO REPRESENT THE TWO ORIGINS OF THE FLEXOR DIGITORUM BREVIS MUSCLE

The arrow indicates the probable method of transference of the origin of the muscle from long flexor tendon to calcaneus. (After Keith, 1929.)

caneus and plantar aponeurosis has occurred phylogenetically. In other words, the deep head seems to exhibit a tendency to become united with the superficial. Notwithstanding the fact that the entire muscle shows individual variability in all the families of Primates, as would naturally be expected, its general characteristics in the various groups are quite apparent. Thus, in the usual condition among prosimians and monkeys the tendon for toe II is derived entirely from the superficial head (i. e., from the plantar aponeurosis or calcaneus, or from both), with the remaining toes (the hallux

dons for both II and III being nearly always derived from the superficial head alone, and that for IV not infrequently. A superficial origin for the fourth toe tendon occurs most frequently by far in the orang (see Table 2). The tendon for the little toe apparently occurs as an element of the superficial layer only in man (large majority) and in the orang (occasionally). Very rarely in monkeys, as in Bischoff's anomalous *Callithrix* (*Hapale*) *penicillata*, and in one of Sawalischin's seven specimens of *Pithecius irus*, the fifth toe tendon may arise at least in part from the superficial head. As far as the

flexor digitorum brevis is concerned the orang more closely approaches man than do the chimpanzee and the gorilla. In man all of the short flexor tendons usually arise from the calcaneus, with a slight attachment to the under side of the plantar aponeurosis; the deep head is normally entirely absent (transferred to the calcaneus), but in a small percentage of cases it may be present in that the tendon for toe V may be derived in whole or part from a small

from a small muscle-belly on the undivided *flexor tibialis* tendon (deep head) in four cases (33.3 per cent), entirely from the calcaneus and plantar aponeurosis (superficial head) in five cases (41.7 per cent), and completely absent in three cases (25 per cent). The tendon for toe IV may also have a partial deep origin in 2 per cent of Europeans (2 out of 100) according to Schulze, and in 8.3 per cent of Negroes (1 out of 12), according to my series. Simi-

TABLE 2

Degree (per cent) of transference of origin of the separate digital tendons of the *flexor digitorum brevis* muscle from the tendon of the *flexor tibialis* muscle to the calcaneus and plantar aponeurosis, in some representative Primates. It should be noted that the transference begins at the inner side of the foot and progresses rather gradually towards the outer. The gorilla and chimpanzee have reached approximately the same stage in the evolution of the muscle, but the orang-utan, however, even more closely approaches the human condition (practically complete transference to calcaneus). This is a parallel specialization of the orang foot not found in its other muscles. Absence of a tendon has been regarded as non-transference. Based on data collected by the author from the literature and from his own dissections

	NO. SPEC.	TOE II			TOE III			TOE IV			TOE V		
		Partial Trans.	Complete Trans.	P. + C. Trans.	Partial Trans.	Complete Trans.	P. + C. Trans.	Partial Trans.	Complete Trans.	P. + C. Trans.	Partial Trans.	Complete Trans.	P. + C. Trans.
Man.....	69	0	100	100	3	97	100	4	96	100	0	78	78
Gorilla.....	15	0	100	100	27	73	100	7	7	14	0	0	0
Chimpanzee.....	28	4	93	97	79	18	97	29	0	29	0	0	0
Orang-utan.....	24	0	92	92	8	92	100	33	21	54	4	17	21
Gibbon.....	21	14	86	100	5	0	5	0	0	0	0	0	0
<i>Pithecus</i>	13	15	85	100	31	0	31	15	0	15	8	0	8
<i>Pygathrix</i>	13	23	77	100	8	0	8	0	0	0	0	0	0
<i>Cebus</i>	8	0	100	100	25	0	25	0	0	0	0	0	0
<i>Callithrix</i>	11	27	64	91	18	0	18	0	0	0	9	0	9
<i>Galago</i>	9	0	78	78	0	0	0	0	0	0	0	0	0

muscle-belly associated with the undivided tendon of the *flexor tibialis*. This condition occurs in 11 per cent of cases (11 out of 100) according to Schulze (1867); in 10 per cent of cases (5 out of 50) according to Turner (1867); and in 5 per cent of cases according to Keith (1929). The work of Schulze and Turner was done on Europeans. As to the source of Keith's figure, I am unable to give information. In a small series of Negroes (twelve feet) I found the fifth toe tendon arising entirely

larly, the tendon for III may have a partial deep origin: in 1 per cent of Europeans (1 out of 100), according to Schulze; in 2 per cent of Europeans (1 out of 50), according to Turner; and in 8.3 per cent of Negroes (1 out of 12), according to my notes.

There is therefore, as already stated, a distinct tendency among Primates for the *flexor digitorum brevis* to assume a superficial origin. In the three great apes we see this muscle in stages intermediate between the conditions usual in monkeys and that

normally found in man, stages similar to those through which this muscle probably passed at some period of man's evolution.

If we express the transference of the origin of the tendons mathematically, we obtain some idea of the degree in which the gorilla approaches man. Thus, in the fifteen gorillas, the tendon for toe II always arises entirely from the calcaneus (and plantar aponeurosis); that for toe III has undergone complete transference to the calcaneus in 73.3 per cent (11 animals) and partial transference in the remaining 26.7 per cent (4 animals), so that in no

suggests a primary connection of the short flexor of the toes with the long flexors. It offers an explanation for those cases in which part of the muscle arises from the long flexor tendon.

M. flexor tibialis and *M. flexor fibularis* (fig. 22). These muscles are most profitable considered together, for in the gorilla they are practically always more or less united in the sole, and a single digit is frequently supplied by both. The distribution of the tendons in the various specimens investigated is given in table 2. The hallux is supplied exclusively by the

TABLE 3

Distribution of the long flexor muscles in gorillas, with reference to the origin of the long flexor tendons

AUTHOR	FLEXOR FIBULARIS	FLEXOR TIBIALIS
Bischoff.....	1 2 3 4 5	2 5
Chapman.....	1 3 4	2 5
Deniker (fetus).....	1 3 4	2 5
Deniker (juvenile).....	1 3 4 5	2 5
Duvernoy.....	1 3 4	2 5
Hartmann.....	1 3 4	2 5
Hepburn.....	1	2 3 4 5
Huxley.....	1 3 4	2 5
Macalister.....	1 2 3 4	2 3 4 5
Owen.....	1 3 4	2 5
Pira.....	1 2 3 4	5
Rothschuh.....	1 3 4	2 3 4 5
Sommer.....	1 (5)	2 3 4 5
No. 47.....	(1)(2) 3 4 5	1 2(3)(4)

specimen is this tendon derived wholly from the deep layer; the tendon for toe IV has entirely migrated in only 6.7 per cent (1 animal), and partially in 6.7 per cent (1 animal) also, while in the remaining 86.6 per cent (13 animals) no transfer has taken place. The tendon for V, when ever present, arises entirely from the deep head.

In the foot of a human embryo of 20 mm. C. R. length, Bardeen (1907) found the *flexor digitorum brevis* anlage associated with the surface of the aponeurosis of the long flexor muscles. This, it seems to me,

fibular flexor in all of the lowland gorillas, but in the highland gorilla (No. 47) most of the great toe tendon is derived from the tibial flexor. The second toe is usually supplied by the tibial flexor alone (Chapman, Deniker: fetus, Deniker: juvenile, Duvernoy, Hartmann, Hepburn, Huxley, Owen, Roths Schuh, Sommer), but sometimes by both flexors (Bischoff, Macalister, No. 47), or by the fibular flexor alone (Pira). Usually the third toe tendon is derived only from the *flexor fibularis* (Bischoff, Chapman, Deniker: fetus, Deniker: juvenile, Duvernoy, Hartmann, Hux-

ley, Owen, Pira), but it may be supplied by both flexors (Macalister, Roths Schuh, No. 47), or from the *flexor tibialis* alone (Hepburn, Sommer). The fourth toe tendon is also customarily derived from the *flexor fibularis* (Bischoff, Chapman, Deniker: fetus, Deniker: juvenile, Duvernoy, Hartmann, Huxley, Owen, Pira), but it may come from both flexors (Macalister, Roths Schuh, No. 47), or only from the *flexor tibialis* (Hepburn, Sommer). The fifth toe is nearly always provided for by the tibial flexor solely (Chapman, Deniker: fetus, Duvernoy, Hartmann, Hepburn, Huxley, Macalister, Owen, Pira, Roths Schuh), or by both flexors (Bischoff, Deniker: juvenile, Sommer), or else by the fibular flexor entirely (No. 47). It will be noted that the *flexor fibularis* tends to supply the first, third and fourth toes exclusively, while the *flexor tibialis* is confined to the second and fifth toes. A similar arrangement is found in most chimpanzees and orang-utans (Kohlbrugge), although in the latter ape the long flexor tendon for the hallux is nearly always missing, this probably being a degenerative specialization which is merely a manifestation of the reduction of that digit in the orang. But the distribution of the long flexor tendons in the great apes can hardly be as simple as the tables of Kohlbrugge (S. 202-203) and myself (table 3) indicate. While there are, of course, many cases among the anthropoids in which no connection between the long flexors occurs (in my orang there was no connection whatsoever between the tendons, the fibular supplying III and IV and the tibial II and V; also see Glaesmer, 1910, on this point), yet, in the gorilla at least, this is by no means the rule (in my chimpanzee the fibular flexor supplied all of the tendon for I and the major portions of those for III and IV, the tibial all of those for II and V, and sent a strong slip

to augment the fibular tendons for III and IV). Thus, Chapman, Deniker, Duvernoy, Hartmann, Hepburn, Huxley, Pira and Sommer all note that the long flexors of their gorillas have tendinous connections in the sole,—findings which of course can only mean that some of the digits were supplied by both flexors. Yet none of these writers indicates a dual tendon supply for any of the toes (except for the fifth toe in Deniker's juvenile and Sommer's gorilla). There can be but little doubt that the distribution of the long flexor tendons in all of these animals was much more complex than the accounts of the investigators indicate. In the gorillas of Bischoff, Macalister and Roths Schuh, and in No. 47, some of the lateral toes receive tendinous elements from both long flexors. Owen indicates the usual simple anthropoid ape type of distribution, and does not mention any connection between the tendons. As already stated, Kohlbrugge's table indicates that in the three great apes the *fl. fibularis* is usually confined to toes I, III and IV, and *fl. tibialis* to II and V (that for I not normally occurring in the orang). But, I would repeat, there is evidence that a mingling of fibres of the two primary flexor tendons occurs very frequently (as in my chimpanzee), and this is certainly the case in nearly all gorillas.

In man, the *fl. fibularis* (*fl. hallucis longus*) has concentrated chiefly upon the hallux, while the *fl. tibialis* (*fl. digitorum longus*) is divided to the four lateral toes, and only occasionally contributes to the formation of the hallucal tendon. Schulze (1867) and Turner (1867) studied the distribution of the long flexor tendons in Europeans in 100 and 50 examples respectively. Schulze found that the *flexor fibularis* always supplied the hallux and the second digit. It went to toes I and II alone in 32 per cent (32 cases); to I, II and III in 58 per cent

(58 cases); and to I, II, III and IV in 10 per cent (10 cases). He found the *flexor tibialis* always supplying the three outer digits. It contributed to the tendon for toe II in 98 per cent (98 cases), and to that for the hallux in 29 per cent (29 cases). The hallucal tendon, therefore, was in 71 per cent supplied by the *fl. fibularis* alone, in 29 per cent by both muscles; the tendon for II in 2 per cent by the *fl. fibularis* only, in 98 per cent by both flexors, the tendon for III in 32 per cent by the *fl. tibialis* alone, in 68 per cent by both; the tendon for IV solely by the *fl. tibialis* in 90 per cent, by both in 10 per cent; and the tendon for V in 100 per cent by the *fl. tibialis* alone. Turner obtained essentially similar results. In his group the *flexor fibularis* always went to the first and second digits. It went to toes I and II alone in 22 per cent (11 cases); to I, II and III in 40 per cent (20 cases); to I, II, III and IV in 36 per cent (18 cases); and to I, II, III, IV and V in 2 per cent (1 case). The *flexor tibialis* in every instance sent fibres to III and IV, and in 98 per cent (49 cases) to V. In the one foot in which the tibial flexor failed to reach the fifth toe, the perforating tendon of that digit was derived entirely from the *quadratus plantae*. The *fl. tibialis* likewise supplied toe II in 96 per cent (48 cases), and toe I in 18 per cent (9 cases). The tendon to the hallux, therefore, was supplied solely by the *fl. fibularis* in 82 per cent, by both flexors in 18 per cent; the tendon for II in 4 per cent by the *fl. fibularis* only, in 96 per cent by both; the tendon for III in 22 per cent by the *fl. tibialis* alone, in 78 per cent by both; the tendon for IV by the *fl. tibialis* by itself in 62 per cent, by both in 38 per cent; and the tendon for V in 96 per cent by the *fl. tibialis* alone, in 2 per cent by both. In the twelve Negro feet which I studied the *fl. fibularis* always went to the two tibial digits. It supplied toes I and II only in 25 per cent

(3 cases); I, II and III in 58.3 per cent (7 cases); I, II, III and IV in 16.7 per cent (2 cases). The *fl. tibialis* always supplied the three fibular digits. It also went to toe II in 91.7 per cent (11 cases). The great toe tendon therefore received fibres only from the *fl. fibularis* (100 per cent); the tendon for II only from the *fl. fibularis* in 8.3 per cent, from both flexors in 91.7 per cent; the tendon for III solely from the *fl. tibialis* in 25 per cent, from both in 75 per cent, the tendon for IV only from the *fl. tibialis* in 83.3 per cent, from both in 16.7 per cent; and the tendon for V always solely from the *fl. tibialis* (100 per cent). These results agree essentially with those obtained by Schulze and Turner on Europeans. Although my present series is quite small, I have thought it worth while to include it here, since it is composed entirely of Negroes. In man, therefore, there is a decided tendency for the *fl. fibularis* to become restricted to the hallux, and for the *fl. tibialis* to assume control of the other toes. The tibial flexor has not as yet, however, begun to eliminate the fibular element in the second digit. The usual human type of arrangement of the long flexor tendons is not normally found in any other Primate. Macalister's gorilla, however, exhibits an arrangement not infrequent in man. The distribution of the tibial flexor in my chimpanzee somewhat suggests the usual arrangement in man. In most gibbons the fibular flexor is distributed to the four inner toes, the tibial flexor being confined chiefly to the second and fifth, but it may also contribute to the formation of other tendons, notably that to the hallux (Kohlbrugge, Glaesmer). In both man and gibbon the tendon to the hallux not infrequently contains a tibial element, and that to the second toe always contains fibular fibres. These are primitive characters, in contrast to the arrangements for

these toes in the three great apes. Some monkeys show a definite approach to the anthropoid ape type of arrangement, the *flexor fibularis* supplying toes I, III and IV and the *flexor tibialis* II and V. But in practically all monkeys, as in gibbons and prosimians, the hallucal tendon is derived from both muscles, and other digits (notably the fourth) often receive a double supply also (Pagenstecher, Kohlbrugge, Glaesmer). In *Pygathrix germaini* I found the *fl. fibularis* supplying all of the tendons for III and IV, and that for I in common

the fifth. Zuckerkandl found a quite advanced condition in his specimens of *Daubentonia madagascarensis* and *Galago crassicaudatus*. In these animals the long flexor tendon of the hallux was derived from the *flexor fibularis* alone, while all of the other toes were supplied by both flexors.

It is generally agreed that the fibular and tibial flexors of mammals have been derived phylogenetically from different muscle layers (Eisler, 1895a; McMurrich, 1905; Ribbing, 1909). Both Dobson

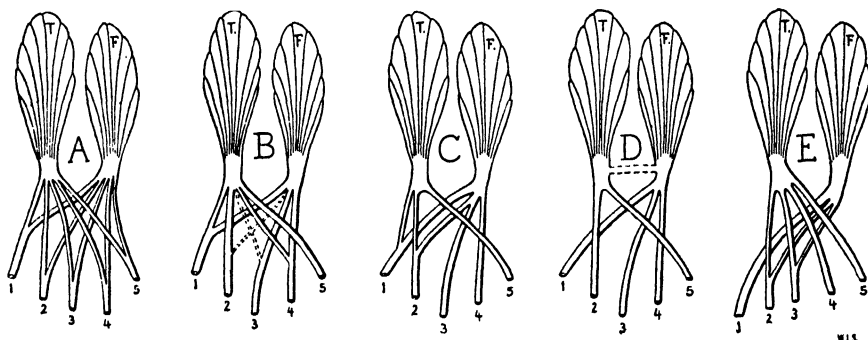


FIG. 22. DIAGRAMMATIC REPRESENTATION OF VARIOUS TYPES OF DISTRIBUTION OF THE TENDONS OF THE FLEXOR TIBIALIS (T.) AND FLEXOR FIBULARIS (F.) MUSCLES IN PRIMATES

A. Most prosimians. B. Most monkeys. C. Most gibbons. D. Most orang-utans, chimpanzees and gorillas (in nearly all orangs, however, the tendon to the hallux is absent). E. Usual arrangement in man. The connecting band, shown by dashed lines, which unites the primary long flexor tendons in diagram D, indicates that one or more of the tendons for the four lateral digits may at times receive fibers from both muscles.

with the *fl. tibialis* and *quadratus plantae*, which muscles also furnish the tendons for II and V. There was no other connection between the long flexor tendons. In most of the prosimians both long flexors are usually rather evenly distributed, the four inner digits usually receiving a dual tendon-supply, (Murie and Mivart, Zuckerkandl, Glaesmer, Straus) while the fifth toe tendon may be from the *fl. tibialis* alone (Zuckerkandl, Glaesmer, Straus), or from both flexors, but chiefly from the tibial (Murie and Mivart, Zuckerkandl). In *Galago* I found the *fl. tibialis* going to all the toes, the *fl. fibularis* to all except

(1883) and Glaesmer (1910) regard the plantar fusion of the two long flexors as the primitive mammalian condition; and their separation as secondary. The opposite view is maintained by Ribbing. The prosimians therefore essentially exhibit what Dobson and Glaesmer regard as a primitive condition, with other Primates showing more advanced arrangements. The fusion of the tendons and their mode of distribution in the highland gorilla (No. 47) suggest the type of arrangement in prosimians and some monkeys.

I do not believe that, among the great apes, the long hallucal flexor tendon has

hitherto been observed to be composed of fibres from both long flexors. This is an arrangement characteristic of the gibbons, monkeys and prosimians (it occasionally occurs, as already cited, in man). Yet even in these animals (including the varieties found in man) the *fl. fibularis* forms at least half of the hallux tendon (except in Schulze's example of *Pithecia*, in which three-fourths of the hallux tendon was from the *quadratus plantae*, the remaining one-fourth from the *fl. tibialis*; and in his *Callithrix* in which the great toe was supplied by the *quadratus plantae* alone), whereas in No. 47 the *fl. tibialis* contributes over three-quarters of the fibres. This predominance of the *fl. tibialis* in the formation of the hallucal tendon occurs also, according to Dobson (1883), in certain Marsupials and Chiroptera, and in the Insectivore *Centetes caudatus*, which he regards as exhibiting the essentially primitive mammalian arrangement of the long flexor tendons. In these animals the *fl. tibialis* predominates in the formation of the tendon to the hallux, sometimes to the virtual exclusion of the *fl. fibularis*.

Participation of the fibular flexor in the tendon for the fifth toe is also unusual among higher Primates. The condition found in No. 47, in which the minimus is supplied only by the fibular flexor, seems to have no parallel among the known great apes; it occurred, however, in Hepburn's gibbon and Meckel's spider monkey (*Ateles*). Glaesmer finds that toe V is supplied only by the fibular flexor in a number of mammals: namely, the Monotremes, some Marsupials, a number of Edentates, and certain Insectivores. I believe that it would be unfair, on the basis of the single known specimen, to state that the highland gorilla differs from the lowland species in the arrangement of the long flexor tendons. The distribution of the tendons in No. 47 should rather be re-

garded as a variation of very primitive type. These primitive characters in the long flexor tendons of No. 47 are: a) their high degree of fusion, recalling the condition found in prosimians and in other orders of mammals; b) the predominant part played by the *fl. tibialis* in the formation of the hallucal tendon, an arrangement not normally encountered among the Primates, but occurring in some other mammals; and c) the derivation of the outermost tendon from the *fl. fibularis* alone, also an essentially non-Primate condition. For a further discussion of the long flexor muscles in Primates the reader is referred to Keith (1894, 1929).

In conclusion, it must be mentioned that the long flexor tendons of Primates are not entirely formed by fibres from the *fls. fibularis et tibialis* alone. The *quadratus plantae* may contribute considerable tendinous elements to certain of the long flexor tendons. This phenomenon will be discussed in the following section.

M. quadratus plantae (fig. 23). This muscle, the *flexor accessorius* or *caro quadrata* of the older anatomists, is not always present in the gorilla. It has been found by Hepburn, Huxley, Macalister, and Owen. In the specimen of Huxley it is described as well-developed, in those of Hepburn and Macalister it was feeble and small, while Owen merely notes its presence. Bischoff, Chapman, Deniker (2 animals), Pira and Sommer definitely state that the *quadratus* was missing. Hartmann does not commit himself as to its absence or presence. The muscle is neither mentioned in the text nor figured in the plates of Duvernoy. I have found not a trace of this structure in a lowland gorilla (No. 1105), nor in the highland example (No. 47). If we regard it as absent in the animals of Duvernoy and Hartmann—and I have no hesitation on this score—we find the *quadratus plantae*

present in only 30.8 per cent (4 out of 13) of the lowland gorillas; add to this list No. 47, and it occurs in only 28.6 per cent (4 out of 14) of all gorillas. According to the figures collected by Keith (1899), it was present in six out of ten gorillas (60 per cent). As to its occurrence in other anthropoid apes (after Kohlbrugge): present in seven out of fourteen chimpanzees (50 per cent); present in six out of thirteen

find it in *Cebus fatuellus*). This muscle is always lacking in lemurs (i.e., lacking in all those examined by Glaesmer, Murie and Mivart, Ribbing, Weidenreich, Zuckerkandl and Straus). Burmeister, Duckworth, Ribbing and Woollard did not find it in *Tarsius*. I found no *quadratus plantae* in the orang, *Hylobates pileatus* and *Galago*. It was present in both the chimpanzee and *Pygathrix germaini*. In

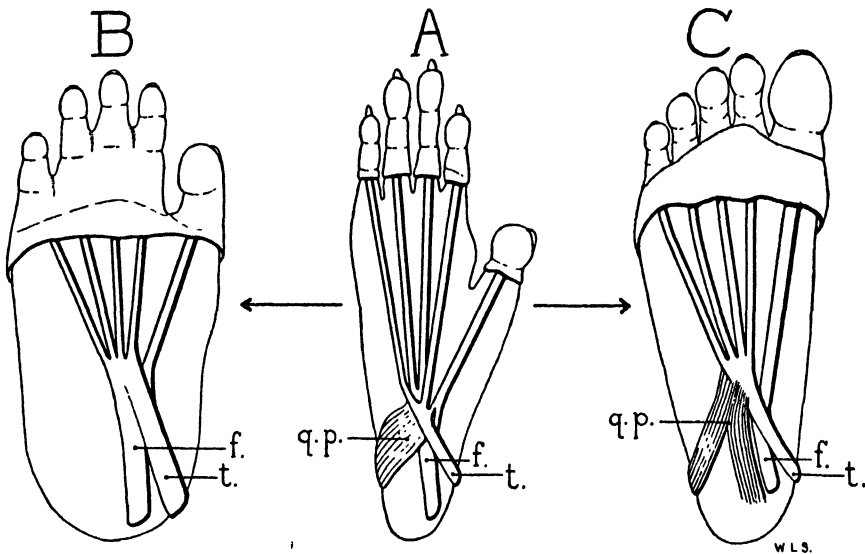


FIG. 23. TWO DIRECTIONS OF EVOLUTION OF THE QUADRATUS PLANTAE MUSCLE IN PRIMATES

A. Primitive type, consisting of a single lateral head, as in both New and Old World monkeys and some orang-utans, chimpanzees and gorillas. B. Complete absence, as in all prosimians, rarely in monkeys (one case), all gibbons, some orangs, chimpanzees and gorillas, and rarely in man. C. two-headed type, as in man (large majority) and rarely in orang (one case). q. p. = quadratus plantae; f. = flexor fibularis tendon; t. = flexor tibialis tendon.

orangs (46.2 per cent); and always absent in the gibbons (8 examples). Keith (1899) states that it was present in six out of eleven chimpanzees (54.5 per cent). This muscle is but rarely completely absent in man (Le Double).

The *quadratus plantae* is always found in Old World monkeys (Bischoff, 1870; Glaesmer; Kohlbrugge; Ribbing; Straus). It is also normally present in the New World forms (Ribbing did not, however,

these it was a single-headed muscle arising from the outer surface of the calcaneus. According to Glaesmer, Leche and Ribbing, it may be absent in some other mammals, e.g., some Insectivores, most Chiroptera, Ungulates, some Edentates, Carnivores and Rodents, and most Marsupials.

In all Primates except man the muscle consists of but a single head (Kohlbrugge), which usually arises from the lateral side

of the calcaneus. However, Hafferl (1929) has recently described a two-headed *quadratus plantae* in an orang-utan.

Kohlbrugge notes that the origin is sometimes, on the other hand, from the medial instead of the lateral side of the calcaneus, e.g., in some chimpanzees and constantly in his *Colobinae* (*Semnopithecus*). The muscle arose from the medial side in four of the chimpanzees studied by Fick (1925); it was absent in the fifth animal. In both *Pygathrix germaini* (which is a representative of the sub-family *Colobinae*) and the chimpanzee I found it arising only from the lateral side of the bone. I have noticed, in man, that the lateral head of the muscle may at times be largely tendinous and smaller than the medial head. According to Weidenreich, this is the rule in fetuses. It is the lateral head which is most frequently absent in man, the medial seldom being lacking (Le Double). Weidenreich regards the medial head of the human muscle as homologous with the deep head of the *flexor digitorum brevis* of other mammals.

When present, the *quadratus plantae* inserts fleshily on the long flexor tendons, and in addition contributes to the formation of certain of these tendons through the medium of tendinous elements. In man, these contributions are given, as a rule, according to Schulze, to the long flexor tendons for toes II, III and IV, and also in 40 per cent of all cases to that for V. Customarily, in his specimens, most of the *quadratus* tendon went to those for III and IV, and a smaller portion to II; when part went to V, this was usually small. In one foot (1 per cent) Schulze saw a not insignificant tendon bundle of the *quadratus* going to the tendon for the hallux. The perforating tendon for II usually derived one-fifth of its fibres from the *quadratus*; that for III one-third; that for IV one-third; and that for V received

varying amounts up to as much as one-third of its volume. Turner found essentially the same arrangement of the *quadratus plantae* in his series. The muscle usually contributed to the perforating tendons of toes II, III and IV, and often to that of V. He found that in a few cases the long flexor tendon for V was almost entirely formed by the *quadratus*, and in one foot (2 per cent) this tendon was apparently entirely thus constituted. In one case (2 per cent) it also sent some fibres to the hallucal tendon. The *flexor digitorum brevis* tendon for toe III also received fibres from the *quadratus* in one instance. In twelve Negro feet I found the *quadratus plantae* always contributing to the perforating tendons for III and IV; to that for II in 9 (75 per cent); and to that for V in 5 (41.7 per cent). Twice it formed the major portion of the tendon for V; twice in the case of that for IV; and once in the case of that for III.

Apparently no data on the distribution of the *quadratus plantae* tendon in anthropoids are available. In the chimpanzee which I examined the muscle did not reach the flexor tendons, but ended in the adjacent ligamentous tissue. Humphry (1867) found the same condition in one of his chimpanzees. Among Old World monkeys Schulze found that the tendinous portion of the *quadratus plantae* was distributed to the long flexor tendons for toes II, IV and V in *Papio* (*Cynocephalus*) *porcarius* (2 specimens), or only to those for II and V in *Erythrocebus patas* (*Cercopithecus ruber*) and 2 examples of *Lasiopyga* sp.? (*Cercopithecus* sp.?). Pagenstecher found that the *quadratus plantae* joined the *flexor fibularis* tendons to toes I, III and IV in *Papio leucophaeus* (*Mandrilla leucophaea*). In *Pygathrix germaini* most of the fibres go to the tendon for toe II, a lesser number to that for V, and the smallest portion to the tendon for the hallux through the *β*.

tibialis element to that toe (Straus). In New World monkeys Schulze noted that the quadratus tendon was divided to toes IV and V in *Ateles*, to II and V in *Saimiri sciureus* (*Chrysotrich sciurea*), to V alone in *Cebus capucinus*, and to I only in *Pithecia chiropotes* (*rufimana*) and *Callitrich jacchus* (*Jacchus vulgaris*). Whereas in Schulze's Old World forms the quadratus plantae always contributed only a minor portion to the respective tendons, in *Pithecia* it formed three-fourths of the hallux tendon (the remaining one-fourth coming from the *fl. tibialis*) and in *Callitrich* the entire tendon for the great toe.

Mm. lumbricales. There is not a great deal to say about these muscles in the gorilla. They are usually disposed as in man, four nearly always being present (Bischoff, Duvernoy, Hepburn, Pira, No. 1105, No. 47), but they may number only two (Huxley). They appear always to arise from the long flexor tendons. The three lateral arise by two heads and the medial by one, as in man (Duvernoy, Hepburn, No. 47), but in one animal only that for toe IV was two-headed (Pira). Their insertions are as in man (Duvernoy, Hepburn, Pira, No. 47). Deniker and Sommer state that the *lumbricales* did not differ from those of the human foot. They are powerful, well-developed muscles in the gorilla (Bischoff, Chapman, Hartmann, Owen, No. 47).

The *lumbricales* usually are four in number in the other anthropoids and in monkeys. In prosimians they likewise customarily number four, but there may be only three in *Nycticebus coucang* (*tardigradus*) (Murie and Mivart), *Perodicticus*, and some *Indrisinae* (Ribbing), or as many as seven in *Loris* (*Stenops*) *tardigradus* (Glaesmer) and *Tarsius* (Allen), and their insertions are sometimes more complex than in other Primates. Burmeister, Ribbing and Woollard each describe four for *Tarsius*. Single-headed *lumbricales* are

not very uncommon in the orang (usually the case for toes II, IV and V), and also occasionally occur in the gibbons and *Colobinae* (Kohlbrugge). In my orang all except that for digit III arose by only single heads from the tibial sides of the respective long flexor tendons. The two medial muscles were single-headed in my chimpanzee. In the *Pygathrix germaini* those for II and V arose by single heads. The two peripheral ones were one-headed in the galago. Murie and Mivart found that all four were single-headed in *Lemur catta*. In man, one or more *lumbricales* may be absent; their origins may vary, or the insertions may be bifurcated (Le Double).

M. tibialis posterior. The insertion of this muscle varies in different specimens of gorilla. It may be into the *naviculare* and the cuneiforms (Duvernoy), the lower part of the *naviculare* and *cuneiforme III* (Hepburn),¹ *naviculare*, *cuneiforme I* and head (base?) of *metatarsale III* (Macalister), *naviculare*, all three cuneiforms and *metatarsalia I* and *II* (Pira), tuberosity of *naviculare*, *cuneiforme I*, cuboid and sheath of *peroneus longus* (Sommer), or tuberosity of *naviculare*, the cuneiforms, *sustentaculum tali* and sheath of *peroneus longus* (No. 47). Keith (1929) states that the *tibialis posterior* in the gorilla ends primarily in the bases of *metatarsalia II, III and IV* and in the ligamentous tissues at their bases, while the attachment to the *naviculare* and the inner side of the foot is only partial and secondary. (In the highland gorilla (No. 47), however, the insertion on the tuberosity of the *naviculare* is most marked, and in Sommer's gorilla this attachment was the primary one.) Furthermore, he states that a similar mode of insertion is found in all Primates except man.

The muscle inserts in man on the tuberosity of the *naviculare*, *sustentaculum tali*,

the three cuneiforms, cuboid, and the bases of the three middle metatarsals, and it is somewhat connected with the sheath of the *peroneus longus* tendon (Bryce). It has been observed to be missing in man, or it may be doubled, forming a so-called "*tibialis secundus*" (Le Double).

For a detailed account of the *tibialis posterior* in other Primates, the reader is referred to Forster (1922). In the chimpanzee the tendon inserts chiefly on the *naviculare* tuberosity, but there is likewise a strong attachment to the two outer cuneiforms (Forster, Hepburn, Straus). In the orang the insertion is on the *naviculare* tuberosity, the three cuneiforms and sheath of *peroneus longus* (Straus), or only on the *naviculare* and peroneal sheath (Hepburn). Forster found that the *naviculare* insertion in his orang was not as strong as the attachment to the cuneiforms. The attachments of the tendon vary among the gibbons. In *Hylobates pileatus* the muscle inserts by a strong tendon on the under side of the *naviculare*, and also sends a tendinous sheet to the two outer cuneiforms, cuboid, and the bases of the three middle metatarsals (Straus); in *H. lar* part of the tendon inserts on the *naviculare*, the rest on the calcaneus, cuboid, and the two outer cuneiforms (Forster); in *H. agilis* the insertion is on the *naviculare* tuberosity and the two outer cuneiforms (Kohlbrugge); and in *Symphalangus (Hylobates) syndactylus* the tendon goes to the *naviculare* tuberosity and *metatarsale III* (Kohlbrugge). Hepburn found the insertion to be on the *naviculare*, sheath of *peroneus longus*, and plantar ligaments in his gibbon.

The insertion in *Pygathrix germaini* is partly on the *naviculare* tuberosity, and chiefly on *cuneiformia II* and *III* and the *peroneus longus* sheath (Straus). In both Old and New World monkeys (see Forster, Kohlbrugge, Ribbing, Rosenfeld) the insertion is usually on the *naviculare* and the

two outer cuneiforms, but the former attachment may be relatively slight or altogether absent. The tendon may reach the three middle metatarsals, it may end on the *naviculare*, or it may insert on the *talus*. As a rule, the *naviculare* attachment is secondary, as Keith (1929) has pointed out, and it is not usually as strong in monkeys and anthropoid apes as it is in man.

In *Galago* the tendon ends on the *naviculare* (Straus). This is the rule in most prosimians (Allen, Burmeister, Forster, Murie and Mivart, Ribbing, Woollard), but the tendon sometimes reaches one or more cuneiforms (Forster, Glaesmer, Milne Edwards and Grandidier, Murie and Mivart, Ribbing, Rosenfeld), and also the bases of the second and third metatarsals (Rosenfeld).

M. flexor hallucis brevis. Two distinct heads are usually present in gorillas (Bischoff, Deniker, Duvernoy, Hartmann, Hepburn, No. 1105). The fibular head may, however, be missing (Pira, Sommer), or it may be united with the oblique adductor (No. 47). Perhaps the fibular head was actually not absent in the animals of Pira and Sommer, but may have been fused with the adductor as in No. 47. The heads usually have distinct origins. The tibial head may arise from the *naviculare* and *cuneiforme I* (Duvernoy, Pira), or from these two bones and the sheath of the *peroneus longus* tendon in addition (No. 47), or from the peroneal sheath alone (No. 1105), or from the *cuneiforme III*, peroneal sheath and from the ligamentous structures between this and the tendon of the *tibialis posterior* (Hepburn), or from the end tendon of the *tibialis posterior* (Sommer). The fibular head arises from the outer border of the hallual metatarsal bone (Bischoff, Duvernoy, Hepburn, No. 1105), or from the first and second cuneiforms and the *peroneus longus*

sheath (No. 47). What is clearly the fibular head is described together with the plantar interossei by Duvernoy. There is nothing of particular interest about the insertions—the tibial head usually inserts with the abductor of the great toe, the fibular with the adductor. Part of the tibial head may insert on the inner border of the shaft of the first metatarsal, forming an *opponens hallucis* (Hepburn, No. 47). The accessory short flexor of the hallux found by Deniker in his gorilla fetus has already been discussed with the *flexor digitorum brevis*.

The *flexor hallucis brevis* has, in general, a similar structure in other Primates. In man the two heads are products of a single belly of origin. It is often inseparably fused with the adductor (Bryce). The tibial head is steadily larger than the outer (Kohlbrugge), which may be fused with the adductor (orang, described by Ruge, 1878b).

There are usually two heads present in monkeys (Kohlbrugge; Ruge, 1878b). Bischoff (1870) found the *flexor hallucis brevis* composed of two heads in all of the Old and New World monkeys which he studied.

Among prosimians, only the tibial head is present in *Lemur* (Cunningham), only the fibular in *Galago crassicaudatus*, *G. alleni* and *G. garnetti* (Murie and Mivart). Apparently these last-named investigators found both heads in *Lemur catta*. Two heads are described by Woollard in *Tarsius*, but only one (the fibular) by Burmeister.

M. opponens hallucis. This muscle is a derivative of the tibial head of the *flexor hallucis brevis*. It was present merely as an attachment of some of the fibres of the tibial head of the *flexor brevis* to the distal half of the inner border of the shaft of *metatarsale I* in Hepburn's gorilla. A somewhat similar arrangement occurs in No. 47, but the insertion is much less

extensive than in Hepburn's animal; in fact, in my specimen the muscle is exceedingly rudimentary, and probably was almost, if not entirely, functionless. Hartmann speaks of an *opponens hallucis* in his gorilla as if it were a separate muscle, and Macalister does likewise. The latter states that it "inserted into the metacarpal bone." I am not quite certain that the muscles described by Hartmann and Macalister under the name of *opponens* of the great toe can really be regarded as such, especially since details of their insertions are not given. The muscle which Macalister calls the *opponens* may possibly be the fibular head of the *flexor hallucis brevis*. A true *opponens hallucis* must so insert on *metatarsale I* that its contraction produces opposing action of that toe. The fibres of the *adductor hallucis* which frequently insert in anthropoids on the outer border of the first metatarsal have been regarded by some writers as constituting an *opponens hallucis* ("adductor opponens"), but this clearly is a misnomer. Opposition of the hallux by action of such an adductor is impossible. Bischoff, Deniker, Pira and Sommer found no *opponens hallucis*, and there was none in No. 1105. Chapman, Duvernoy, Huxley and Owen make no mention of such a muscle. There can be little doubt that a well-developed *opponens hallucis* is, at best, very rare in the gorilla. I hesitate to estimate the percentage frequency of its occurrence with the unsatisfactory data now at hand.

The *opponens* is an almost constant occurrence in the orang, in which it may be a separate muscle, arising from the tarsal bones and inserting on the lateral edge and under surface of the first metatarsal, as in Bischoff's (1870) animal, or else still attached to the *flexor hallucis brevis*, and inserting in the inner border of the hallucal metatarsal, as in the orangs of Hepburn, Primrose and Straus. The *opponens* of

the great toe is extremely rare in other Primates. It may sometimes occur as a separate structure in man (Le Double). Hartmann found "a slightly developed opponens" in a gibbon. I can find no reference to it in chimpanzees. It occurs only occasionally in Old World monkeys, e.g., in the *Pithecus* (*Macacus*) studied by Bischoff, in which it was a separate muscle arising from the tarsus, and in the *Papio cynocephalus* (*Cynocephalus babuin*) of Michaelis, where it originated from the first cuneiform. Kohlbrugge notes its absence in his *Colobinae*. Apparently this muscle does not occur in either New World monkeys or prosimians.

M. adductor hallucis. This muscle is the innermost member of the group of contrahentes (adductors) muscles. In gorillas it is usually divided, somewhat as in man, into two distinct heads, oblique and transverse (Bischoff, Chapman, Duvernoy, Hepburn, Huxley, Macalister, Owen, No. 47), but it may be a single fan-shaped mass (Pira, Sommer). In Deniker's fetus it was divided into five distinct fascicles laid out fanwise. A somewhat similar arrangement was found in No. 1105, in which the muscle is fan-shaped but divided into three parts. In cases where actual division into oblique and transverse heads occurs, the oblique head arises from the bases and proximal portions of *metatarsalia II* and *III* (Duvernoy), or from the proximal portion of an aponeurotic raphe extending along *metatarsale III* (Hepburn), or from the bases of *metatarsalia II* and *III*, sheath of *peroneus longus* tendon, and fascia over the intervening interosseous muscles (No. 47). The transverse head may take origin from (heads of?) *metatarsalia II-V* (Bischoff). It may arise from the heads of *metatarsalia II-IV* (Huxley) or from the heads of *metatarsalia III* and *IV* (Macalister). Duvernoy found it arising from the ends of *metatarsalia II-IV* and an apo-

neurosis which ran for the length of *metatarsale II*. It took origin from the heads of *metatarsalia II* and *III* and the distal portion of an aponeurotic raphe extending along *metatarsale III* in Hepburn's animal. In No. 47 it arose from the distal parts of the shafts and proximal parts of the heads of *metatarsalia II-IV*, from the associated joint-capsules and transverse metatarsal ligaments, the intervening interosseous fascia, and the deep portion of the *aponeurosis fibularis* (No. 47). Hepburn does not give a detailed description of the origins of the two heads, but his figures make the conditions quite clear. In Pira's animal the adductor arose from *metatarsalia II-IV*, in Sommer's from the bases of *metatarsalia II* and *III* and from a tendinous arch which ran from the base to the head of *metatarsale III*. Deniker's fetal gorilla had the adductor split into five fascicles, which took origin from metatarso-phalangeal joints II, III and IV, the middle of *metatarsale IV*, and the proximal part of *metatarsale III*. In No. 1105 the situation was as follows: the proximal portion of the muscle arose from the proximal part of a tendinous raphe extending from the *peroneus longus* sheath to the metatarso-phalangeal joints and from the middle of *metatarsale II* to the middle of *metatarsale IV*, the middle portion from the intermediate part of that same raphe, and the distal portion from the inner border of the raphe and proximal parts of the heads of *metatarsalia II* and *III*. The muscle usually has the same general insertion, both heads (if two are present, or if not, the single head) attaching to the outer side of the basal phalanx of the hallux. In some cases the fibres may extend to the distal phalanx (Duvernoy) or into the distal portion of the outer side of the first metatarsal (Duvernoy, Hepburn, Pira, No. 1105, No. 47) to form the so-called *adductor opponens*, which is a misnomer.

In such metatarsal insertions the fibres are chiefly or entirely from the distal portion of the muscle (transverse head). There also were some adductor fibres attached to the first metatarso-phalangeal joint in Nos. 1105 and 47.

Since the *adductor hallucis* will be discussed in a later publication dealing with the deep muscles of Primate feet, I shall not enter into any further details here. It will be sufficient to note that this muscle may be a single mass or else be divided into two heads in the other anthropoids, monkeys and prosimians.

In man two distinct heads are present, the transverse being weaker than it generally is in other Primates, and it usually arises from the three lateral metatarsals. Leboucq (1895) describes an anomalous fascicle, in three out of sixty European feet, which he believes to represent the middle portion of the *adductor hallucis* of other Primates. In early stages of human development the adductor is not yet divided into distinct oblique and transverse heads. The definitive adult arrangement is arrived at by a migration of the eventual transverse head from the lateral side of the oblique head to the outer border of the foot, and distally to the heads and joint-capsules of *metatarsalia III-V* (Ruge, 1878c). The transverse head may retain an embryonic position, or it may be entirely absent (Ruge, 1878c; Le Double).

Mm. contrahentes II, IV, V (fig. 24). These muscles, members of the same layer as the *adductor hallucis*, are normally absent in gorillas. They were found completely absent by Bischoff, Deniker, Hartmann, Hepburn, Pira, and Sommer. I found no trace in Nos. 1105 and 47 (the aponeurotic sheet covering the interossei in No. 47 might be regarded, as previously stated, as constituting vestiges of the distal portions of the lateral section of this layer).

Duvernoy does not speak of them, nor are they figured in his excellent plates. An

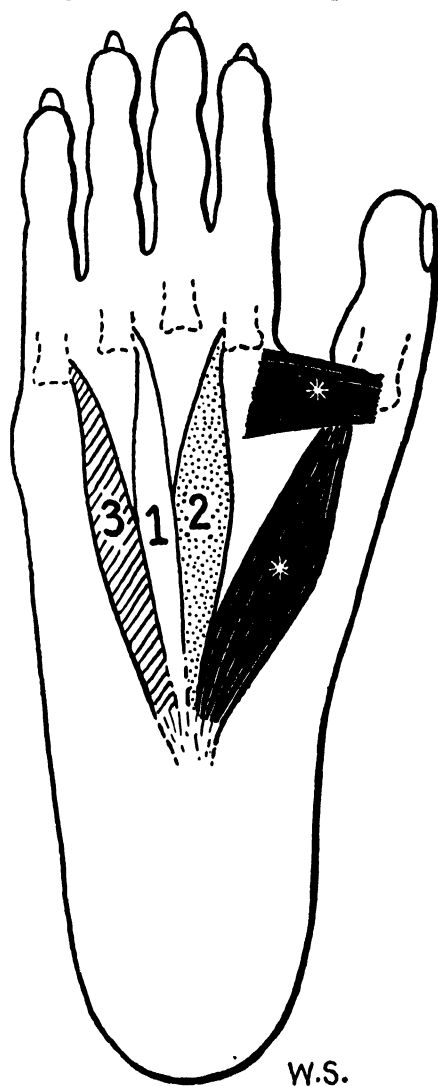


FIG. 24. PHYLOGENETIC ORDER OF DISAPPEARANCE OF THE CONTRAHENTES MUSCLES OF THE FOOT IN PRIMATES

The muscles are numbered in the order of their disappearance. 1 = contrahens digiti IV; 2 = contrahens digiti II; 3 = contrahens digiti V; * = contrahens digiti I (*adductor hallucis*), which is present in all Primates. Based on data collected by the author.

adductor of the fifth toe was present in Macalister's gorilla. This is in all likeli-

hood a *contrahens* V. Keith (1899) states that "the *contrahentes* muscles, either as fibrous bands or as fibro-muscular slips, are always more evident in the Chimpanzee than in the Gorilla." He gives no details, however. The tendinous raphe found in so many gorillas, from which the *adductor hallucis* arises, is the raphe which is associated, in other mammals, with the *contrahentes*.

Since I shall also deal with the *contrahentes* in my forthcoming paper, only a very brief additional reference to them will be made here. In most pentadactyl mammals, as Cunningham (1882) has pointed out, *contrahentes* occur for toes I, II, IV and V, and they are inserted so as to adduct the digits to an imaginary axis through the medius (toe III). This primitive condition persists, as a rule, in prosimians and New and Old World monkeys. Reduction of the three lateral *contrahentes* begins with the gibbons, and is practically completed in the gorilla and man. On the other hand, the innermost member of the group, the *adductor hallucis*, has enlarged greatly and become an important muscle.

Mm. interossei (fig. 25). These are always divided into dorsal and plantar sets in the gorilla. The four dorsal muscles are two-headed (bipenniform), while the plantar arise by a single head. In general the origins are as in man, i.e., each dorsal arises from the plantar surface and side of the metatarsal bone of the digit on which it inserts, and from the dorsal portion of the shaft of the adjacent metatarsal; each plantar arises from the plantar surface and side of the metatarsal of the digit of insertion. There may be a partial origin from the *peroneus longus* sheath, as in No. 47. Insertion of both dorsal and plantar are into the bases of the basal phalanges and the extensor aponeuroses of the toes. The second head of the first dorsal interosseus may arise from

metatarsale I (Hepburn), or from the first cuneiform (Nos. 5 and 47). *Dorsal interosseus* II may arise anomalously by only a single head from *metatarsale* II (Deniker), while *plantar interosseus* I may have two heads of origin, from the adjacent *metatarsalia* (Hepburn), and similarly two heads may be present for *plantar interosseus* II (Deniker). Bischoff's gorilla exhibited a strange arrangement of the interosseous muscles in the right foot, which had two dorsals for the second toe and likewise two dorsals for the fourth toe, while the third digit possessed two plantars; the left foot had the usual gorilline arrangement, with two dorsals for the second toe, one for the third, and one for the fourth. In the gorilla both sets of interossei project markedly into the sole.

By far the most interesting fact in connection with these muscles pertains to their arrangement around the digits. In most gorillas the interossei are oriented so as to ab- and adduct from and to an axis passing through the second toe (Bischoff: left foot, Deniker, Hepburn, Pira, Sommer, Symington, No. 7, No. 47), but in some examples the axis is through the middle digit (Duvernoy, Macalister, No. 5). Thus, in 72.7 per cent (8 out of 11) of gorillas the interosseal axis is through toe II. Keith (1899) in reporting from the literature, states that "in 3 out of 7 Gorillas, the second digit, as is the case in Man, received the insertion of the first and second dorsal interossei muscles." The interossei of Primates will be considered in detail in my paper on the deep foot musculature, and a preliminary report on these muscles has already been published (Straus, 1929a). It is merely necessary again to state here that gorilla and man are the only Primates in which the pedal interossei are usually arranged around the second toe. The human condition may occur as a variation in the other

anthropoids, but apparently in both Old and New World monkeys the axis is always through the third digit, as it is in most pentadactyl mammals. The prosimians show their own type of specialization by often having the axis through the fourth toe, which is usually the longest in these animals. It is interesting to note that both specimens of highland gorilla (Nos. 7 and 47) have the human arrange-

on the adjacent sides of the second and third toes I have found only in the two highland gorillas (Nos. 7 and 47). Only one foot of each animal was available (the left of No. 7, the right of No. 47). I have not thus far encountered an identical muscle in any other animal. I recently saw what appeared to be a partly, if not entirely, similar condition in the left foot of an adult male Negro, in which the inter-

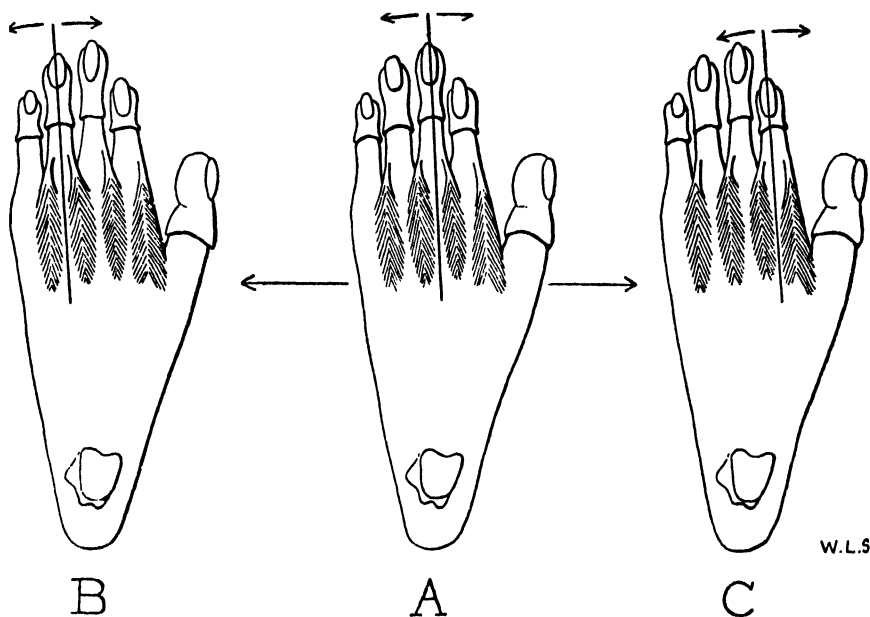


FIG. 25. TWO DIRECTIONS OF EVOLUTION OF THE INTEROSSEOUS MUSCLES OF THE FOOT IN PRIMATES

A. Primitive condition, with axis through third toe, as in all monkeys, some prosimians, most gibbons, orang-utans and chimpanzees, and a few gorillas. B. Axis through fourth toe, as in some prosimians. C. Axis through second toe, as in a few gibbons, oranges and chimpanzees, most gorillas, and all men. Based on data collected by the author.

ment, whereas the lowland gorilla exhibits the usual Primate condition in 33 per cent of the known cases (3 out of 9). In order to decide whether this is really a specific difference, more specimens, especially of the highland form, must be obtained. At any rate, such a difference could only be an average one.

The slip of muscle which arises from the distal portion of the plantar surface of the shaft of *metatarsale III* and splits to insert

ossei were otherwise arranged normally. From the plantar surface of the second dorsal interosseus (for the fibular side of the second toe) there arose distally a fleshy slip about 3 mm. in diameter which was inserted into the tibial side of the metatarso-phalangeal joint-capsule of the third toe. There was no bifurcation to the second toe joint-capsule as in the highland gorillas. The condition described by Ochiltree (1913) in the right foot of an

adult male human, seems to be analogous, if not homologous, with the condition in the *Gorilla beringei*. In reference to the *adductor hallucis*, Ochiltree states that "this muscle possessed an accessory slip which arose from the lateral border of the muscle and was inserted into the adjacent sides of the proximal phalanges of the second and third digits." The muscle-slip in this foot seems, from its association with the adductor (obliquus?) to be the vestige of the contrahens of the second toe (only very occasionally occurring in man), whereas in the two *G. beringei* (and likewise in the Negro) the muscle in question is almost certainly a derivative of the interosseous layer. If we cannot homologize these muscle-slips, at least their general insertions in the two gorillas and the men are the same. The literature, as far as I am aware, contains no accounts of a condition identical with that in my gorillas. It is of course well-known that certain of the *lumbricales* of both hand and foot in man may bifurcate and insert on the two adjacent digits (cf. Le Double on this point). A similar double insertion of one or more *lumbricales* may also occur in other mammals: viz., *Phascogale* (Ribbing), *Manis* (Glaesmer). Perhaps this condition is analogous to that occurring in the two highland gorillas. Eisler (1895b) describes, in the amphibian *Menopoma*, muscles which arise from the distal ends of each metatarsal bone and insert on the basal phalanges; he has seen such a muscle well-developed in a gorilla (certainly a *G. gorilla*, judging from the date of this publication) and also indications of it in man. Possibly this muscle is homologous to that which I have found in my gorillas.

M. flexor digiti V brevis. This muscle arises in the gorilla essentially as in man, from *metatarsale V* and the sheath of the *peroneus longus* (Hepburn, Pira, No. 47).

An additional superficial layer such as I found in No. 47, from the *peroneus longus* sheath, cuboid, and bases of *metatarsalia IV* and *V*, is not mentioned by any other workers (Hepburn, however, notes that it had an additional origin from the base of *metatarsale IV* in his orang). The insertion is on the outer side of the basal phalanx of the little toe (Duvernoy, Hepburn, Pira, No. 47), and in No. 47 there appears to be a slight expansion into the extensor aponeurosis of that toe in addition. It was united with the *abductor digiti V* in Bischoff's specimen, and it inserted with that muscle in Sommer's. The muscle-substance may be pierced by the abductor tendon (No. 47). It is difficult to separate from the third plantar interosseus (Hepburn, No. 47).

The *flexor digiti V brevis*, which is plainly the outermost member of the interosseus series, is a rather constant element of the feet of man and other Primates. In these forms it has the same general origin and insertion. It is never really absent, but it may be entirely converted into an opponens, as in Deniker's gorilla, Ribbing and Hermansson's chimpanzee, and Zuckerkandl's *Daubentonia*.

M. opponens digiti V. This muscle is a derivative of the *flexor digiti V brevis*. In the gorilla it is sometimes present as a portion of the latter (Bischoff, Hepburn, Pira), but it can be a distinct muscle (Deniker). It may be lacking (Hartmann, No. 47). Chapman, Duvernoy, and Macalister, all of whom note the presence of a *flexor digiti V brevis*, do not mention an opponens. In the animals of Bischoff and Pira it was merely represented by certain fibres of the *fl. dig. V brevis* which inserted into the outer border of *metatarsale V*, while in Deniker's fetus a true *fl. dig. V brevis* was absent, the entire muscle having been converted into an opponens. Hepburn found the opponens portion to be

better-developed than the flexor element, the two muscles, however, arising in common. The presence of an *opponens digiti V* has been noted by Sommer, who states that it was united with the flexor at its origin. Yet the muscle which he describes certainly cannot have been a true opponens, for he states that its insertion was on the medial side of the base of the basal phalanx of the fifth toe.

The opponens of the little toe commonly occurs in all groups of Primates. It is found in a majority of men, but merely as a part of the *fl. dig. V brevis*, yet it may occasionally be a separate and independent slip (Bryce). It has also been found in chimpanzee and gibbon (Kohlbrugge), in chimpanzee (Ribbing and Hermansson), in orang and macaque (Le Double), and in a number of prosimians (in *Daubentonia madagascariensis*, *Lemur variegatus* and *Galago crassicaudatus* by Zuckerkandl, and in *Lemur catta* by Murie and Mivart). As I have mentioned, the entire *flexor digiti V brevis* may at times be converted into an opponens.

M. extensor hallucis longus. There is little to say about this muscle. It inserts regularly on the terminal phalanx of the great toe (Hepburn, Owen, Pira, No. 47). Plate IX of Duvernoy shows a similar attachment. Sommer states that the tendon goes into the dorsal aponeurosis of the first toe.

In man and the other Primates the end tendon has a like termination on the terminal phalanx of the hallux (Bischoff, 1870; Murie and Mivart; Zuckerkandl).

Ribbing's researches indicate that the development of this muscle in mammals is roughly proportional to the development of the hallux. In some forms he found it inserting in the second toe. Le Double has listed the types of variation in man; it may insert on both phalanges of the hallux, and it may furnish supernumerary

tendons of various sorts. Similar variations occur in other Primates (Kohlbrugge).

Bardeen states that the *extensor hallucis longus* is to be looked upon as an especially differentiated portion of the *extensor digitorum longus*. In the human embryo, he found its tendon at first fused with the *ext. digit. longus* tendon plate. But even at early stages the muscles may be distinguished from one another.

M. extensor digitorum longus. Customarily in the gorilla it divides into three tendons, the two lateral going respectively to toes V and IV, the medial dividing more distally into tendons for toes III and II (Deniker, Duvernoy, Owen, Pira, Rothschild (quoted by Weidenreich), Sommer, No. 47). Hartmann, Hepburn and Macalister merely note that the muscle supplied the four lateral toes. In Ranke's gorilla tendons were given off for toes II-V. His figure of this muscle (Tafel I) shows two primary tendons, one of which supplies toe V, while the other splits into three distinct parts for digits IV, III and II. In Pira's gorilla there was a *junctura tendinum* between the tendons for III and IV.

The long extensor of the toes usually supplies all of the four lateral toes in man and the other Primates (Ranke, Beattie, Murie and Mivart, Zuckerkandl). Ranke has carefully studied the distributions of the tendons and their connections. His diagrams (Tafel I) show that union of two or more end-tendons is the rule. Whenever any such union occurs, the tendons for toes II and III are always involved and intimately united, a condition which is the rule in the gorilla. In man I have encountered all degrees of separation of these tendons. There are not infrequently only three, as in the gorilla, the innermost later splitting into elements for the second and third toes. This later fusion of the

two most medial tendons is usually, though not always, an accompaniment of webbed toes (zygodactyly) in man (Straus, 1926). It does of course also occur in feet that are not webbed. Weidenreich also discusses this fusion of the tendons, and in great detail. Accessory tendons are not at all uncommon in man, and the muscle is subject to numerous types of variation. Sometimes it has connections with the metatarsal bones, e.g., in a gibbon dissected by Ranke the outermost tendon gave off a slip to the capitulum of *metatarsale IV*. There is no tendon for the second toe in *Lemur variegatus* (*varius*) and *Perodicticus potto* (Murie and Mivart). The second toe tendon was the smallest in No. 47, and Murie and Mivart found the same condition in *Nycticebus coucang* and *Loris tardigradus* (*gracilis*), as did Kohlbrugge in *Colobinae*. It may be missing in the latter and also in the orang (Kohlbrugge, Ranke). There thus seems to be a tendency to reduce or eliminate the supply to the second digit, at least in some forms.

The tendons of the long extensor, upon reaching the digits, continue as elements of the extensor aponeuroses. Willan has carefully isolated the elements of the extensor aponeuroses in man and certain species of baboons (*Papio cynocephalus* (*anubis*), *P. cynocephalus*, *P. sphinx*). Apparently Duvernoy was able to dissect the extensor aponeuroses in his gorilla in greater detail than I have been. Kohlbrugge gives some data on this point for *Hylobates* and *Colobinae*, and Hafferl does likewise for the chimpanzee.

M. peroneus tertius (fig. 26). This muscle is in reality a portion of the *extensor digitorum longus*. It is sometimes present in the gorilla, although so recent a text as Sonntag (1924) does not recognize its existence in this animal. In Rothschuh's (1888) gorilla the muscle was still fleshy distal to the cruciate ligament and was

inserted by a broad tendon to the base of *metatarsale V*. Eisler (1895a) describes what may be regarded as a rudimentary *peroneus tertius* in the right foot of his gorilla; a small portion of the muscle-belly of the *extensor digitorum longus*, fibular to the belly for the fifth toe, passed beneath the cruciate ligament, giving rise to a thin tendon which ran to the middle of *metatarsale V* and could be traced to the capsule of the metatarso-phalangeal joint. The muscle was present as a very definite structure in the gorilla studied by Ranke (1897), who figures it in his Tafel I. In this illustration the muscle-mass of the long extensor of the toes gives rise to three tendons. The innermost of these splits into tendons for the second, third and fourth toes, the middle goes to the fifth toe, and the outermost is the *peroneus tertius*. Details of the insertion are, however, neither given nor pictured. What may be a rudimentary *peroneus tertius* is described by Sommer (1906). In his gorilla the lateral tendon of the long extensor to toe V split into two parts, one going to the dorsal aponeurosis of the fifth digit, while the other was attached on the lateral side of the base of *metatarsale V* and the membrane on the lateral side of this bone from base to head. Morton (1924) describes and figures the *peroneus tertius* in two gorillas. In a young male *Gorilla gorilla* it came from the muscle-mass of the long extensor, but arose from a definite belly; it inserted on the base of *metatarsale V* and was prolonged forward as a thin tendon to the outer side of toe V. This author also describes a *peroneus tertius* in the left foot of an adult female *Gorilla beringei*. This left foot is the mate to the foot which is the subject of the present paper (Comp. Anat. # 47, Amer. Mus. Nat. Hist.). In this left foot Morton found that the *peroneus tertius* tendon came from the common extensor muscle belly, and "the insertion was

located in the outer, upper aspect of the base of the fifth metatarsal bone. Just above this insertion . . . a thin, thread-like prolongation is carried forward to the digit, at a right angle to the tendon proper." I have already given a description of the *peroneus tertius* tendon in the right foot of this same animal. In the right foot, however, there is no thin tendon from the *peroneus tertius* to toe V. At the insertion it is pierced by a narrow tendon prolonged from *peroneus brevis* to the fifth digit (vestige of *peroneus digiti V*). The *peroneus tertius* was absent in the gorillas of Bischoff, Chapman, Deniker, Hart-

structure as Sommer found is possibly a very rudimentary *peroneus tertius* in an early stage of its differentiation from the long extensor. Keith (1923) notes, in respect to the *extensor digitorum longus*, that "in the gorilla one notices occasionally a tendency for the outer fibres of the tendon going to the fifth or small toe to stray or migrate towards the outer border of the foot." The occurrence of the doubled fifth toe tendon in man, even in the presence of a well-defined *peroneus tertius*, might be regarded as an attempt to strengthen this muscle.

A *peroneus tertius*, in some form, occurs therefore in 33.3 per cent of gorillas (6 out



FIG. 26. PERONEUS TERTIUS MUSCLE IN CHIMPANZEE, GORILLA AND MAN, AND AN APPARENTLY HOMOLOGOUS MUSCLE (EXTENSOR TARSII) IN A MARMOSET (*CALLITHRIX JACCHUS*)

p. t. = peroneus tertius; *e. t.* = extensor tarsi. The chimpanzee foot is after Hecker, redrawn; the gorilla foot is after Rothschild, reversed and redrawn from Forster (1916); and the marmoset foot is after Forster (1916), redrawn.

mann, Hepburn, Huxley, Macalister, Pira, and Symington, and likewise in No. 1105. Duvernoy neither mentions nor figures it, nor does Owen, so that one may rightly assume its absence in these animals. Pira claims, and with some justification, that the tendon which Sommer has described as that of a *peroneus tertius* is not actually such a structure. He points out that in man, even when a true *peroneus tertius* is present, the long extensor tendon for V may sometimes be doubled, the extra tendon going to the fifth metatarsal. I have myself seen this in the dissecting room and Morton describes and figures the same condition in his young lowland gorilla. But such a

of 18 animals), if we include the doubtful case of Sommer, or, if we regard Sommer's animal as really lacking this structure, in 27.8 per cent (5 out of 18 animals). In this computation, the two feet of No. 47 described by Morton and myself have of course been treated as a single specimen. In man the muscle varies a great deal in character, and it may be completely absent. It is present in 91.5 per cent of Europeans (Le Double); in 90 per cent (Krause, cited by Sommer). It may send a supernumerary tendon to the fifth toe (Testut, Le Double), as it does in Morton's gorillas.

A well-developed *peroneus tertius* has also been found by Hecker (1922) in a chim-

panzee, but this muscle does not occur in any other Primate. At least, I am not aware that a structure worthy of the name has yet been found. However, Forster (1916) describes a muscle (*M. extensor tarsi*) which inserted upon the outer side of the calcaneus in a specimen of *Callithrix* (*Hapale*) *jacchus*. This muscle, despite its unusual insertion, is most probably homologous to the *peroneus tertius* of man.

Apparently the presence of the *peroneus tertius* in man is not of paramount importance in the economy of the individual, for, as already stated, it is absent in about 10 per cent of cases. It is plainly a progressive structure, and is an attempt to further adapt the foot to the erect posture. Its great variability would suggest that it has, however, not yet attained its fullest development.

M. tibialis anterior. In all gorillas this muscle inserts by separate tendons on the inner aspect of the first cuneiform and on the inner side of the base of the hallucal metatarsal (Bischoff, Deniker, Duvernoy, Hepburn, Macalister, Owen, Pira, Ranke, Sommer, No. 1105, No. 47). In Duvernoy's animal the proximal tendon was also inserted on the *cuneiforme I*-*metatarsale I* joint-capsule, and in No. 47 this same tendon split to give off an accessory insertion into a large sesamoid. The distal tendon of Sommer's specimen was attached to the inner edge of the first metatarsal from base to head. There is considerable variability in the extent of the division of the two insertions. It may involve only the tendon, or the splitting may extend high up into the muscle-belly. In the gorilla dissected by Duvernoy the muscle very early divided into two bellies, so as to form two practically distinct muscles. The belly whose tendon was attached to the base of *metatarsale I* Duvernoy called the "long abductor of the great toe." In No. 47 there is of course no way of ascer-

taining the extent of the splitting, but the muscle-belly was certainly involved, for I found muscle fibres on the plantar surfaces of the tendons. Keith (1899) gives some collected data on the splitting of the tendon and muscle. He states that "of 7 Gorillas, only the tendon was divided in 5; the division extended deeply into the muscle in 2; in the Chimpanzee . . . the muscle and tendon were divided in 16, the tendon only in 3." In the gorilla, the tendon to the first cuneiform is generally much stronger than that to the first metatarsal (Macalister, Pira, Sommer, No. 47). In Macalister's animal the tendon to the hallucal metatarsal was only one-fifth the size of that to the first cuneiform.

In the chimpanzee, as noted above, the division of the muscle is much more complete than in the gorilla. The insertion is limited to *cuneiforme I* and *metatarsale I* (Hepburn, Ranke, Straus). I found the cuneiform insertion to be much the stronger. In Bischoff's chimpanzee (1870) there was also a third insertion on the inner border of the foot.

In man the tendon is usually not divided until just previous to its insertion on the first cuneiform and first metatarsal, but the actual extent of splitting varies. The division may sometimes extend into the muscle-belly, and rarely the entire muscle may be divided in two (Le Double).

The insertion in the orang is *cuneiforme I* and first metatarsal (Hepburn, Ranke, Straus). In my animal the insertion on the cuneiform was the stronger. The extent of splitting varies considerably (Kohlbrugge). It may involve the whole muscle or the tendon alone, but it usually is not as extensive as in the chimpanzee (Sommer).

In the gibbons the muscle usually inserts on *cuneiforme I* and *metatarsale I*. This is the arrangement in *Hylobates leuciscus*, *H. agilis*, and *Symphalangus syndactylus* (Kohl-

brugge), *Hylobates* sp.? (Hepburn), *Hylobates* I (Ranke) and *Hylobates pileatus* (Straus). In Kohlbrugge's specimens there was an additional insertion on a small bone which lay between *cuneiforme* I and *metatarsale* I. The insertion may be limited to *cuneiforme* I (Bischoff's *Hylobates leuciscus*) or to *metatarsale* I (Ranke's *Hylobates* II). The tendon to the cuneiform was much the larger in my *H. pileatus*. Only the tendon may be split, as in *Symphalangus syndactylus* and *Hylobates leuciscus* (Kohlbrugge) and *Hylobates* I (Ranke), or the muscle-belly itself may be divided, as in Hepburn's gibbon.

Metatarsale I and *cuneiforme* I are the points of insertion in Old World monkeys (Kohlbrugge, Ranke, Pagenstecher, Straus). The cuneiform insertion was much the stronger in my *Pygathrix germaini*. Not only the tendon, but also the muscle-substance, at least in part, is always divided (Bischoff, Ranke, Ribbing, Straus). The muscle itself was split only distally in *Pygathrix cristata* (*Semnopithecus maurus*) (Kohlbrugge), and in *Pithecus irus* (*Macacus cynomolgus*), *Simia sylvanus*, *Lasiopyga griseoviridis* (*Cercopithecus sabaeus*), and *Papio cynocephalus* (*Cynocephalus babuin*) (Ribbing); the division of the muscle was complete in *Papio sphinx* (*Cynocephalus maimon*), *Lasiopyga* (*Cercopithecus*), and *Pithecus* (Bischoff), in *Nasalis larvatus* (*Semnopithecus nasicus*) (Kohlbrugge), and in *Papio* (*Cynocephalus*) *hamadryas*, *Pithecus* (*Macacus*) *nemestrinus*, *Erythrocebus patas* (*Cercopithecus ruber*), and *Lasiopyga* (*Cercopithecus*) sp.? (Ranke). In my *Pygathrix germaini* the upper portion of the leg was absent, so that I am unable to state the exact extent of the division. Not only the tendon, but also the portion of the muscle which was present, were entirely divided.

In New World monkeys the muscle usually inserts on both *cuneiforme* I and *meta-*

tarsale I. It may, however, be limited to the first cuneiform, as Kohlbrugge found in *Leontocebus* (*Hapale*) *rosalia*. Both tendon and muscle are usually split, the latter entirely, so that two muscles seem to be present. This was the case in *Pithecia monacha* (*birsuta*) and *Callithrix penicillata* (Bischoff), in *Cebus apella* and *Callithrix* (Ranke), in *Cebus fatuellus* and *Callithrix* (*Hapale*) *jacchus* (Ribbing). The tendon and only the distal part of the muscle-belly may be split, as in *Brachyteles* (*Ateles*) *arachnoides* (Ribbing) and *Alouatta ursina* (*Mycetes fuscus*) (Sirena). The tendon only may be split in *Callithrix* (*Hapale*) *jacchus* (Beattie).

Among prosimians the insertion may be on both the first cuneiform and first metatarsal, as in *Lemur variegatus*, *L. fulvus* (*xanthomystax*) and *L. nigrifrons* (Murie and Mivart), in *Lemur mongoz* (Ranke), in *Lemur mongoz* (Ribbing), and in *Daubentonia madagascariensis* and *Lemur variegatus* (Zucker-kandl). The insertion was only on the first cuneiform in *Tarsius* (Burmeister), in *Lemur catta* (Murie and Mivart), in *Lepidolemur* (*Lepilemur*) and *Tarsius* (Ribbing), in *Tarsius* (Woollard), in *Galago crassicaudatus* and *Loris tardigradus* (*Stenops gracilis*) (Zucker-kandl), in *Propithecus* (Milne Edwards and Grandidier), and in *Galago* (Straus). Both tendon and muscle are completely split in two whenever the insertion is on both cuneiform and metatarsal.

Kohlbrugge points out that in general among Primates the cuneiform insertion is the stronger, as I found in all of my specimens showing double insertions. The original insertion of the muscle in mammals, according to Ribbing, was on the first cuneiform. This would explain the relative weakness of the metatarsal attachment. Viewed in this light, the usual splitting of the muscle among Primates is a secondary phenomenon. Such

a splitting would procure an independence of the two components, an independence which might prove useful to a climbing animal.

Mm. extensores hallucis et digitorum breves. These are merely parts of a single muscle, and may be considered together. In the gorilla they are always united at their origin, which is from the upper and lateral surfaces of the calcaneus (Pira, No. 1105, No. 47). In No. 47 there was a slight additional origin from the under surface of the cruciate ligament. Four more or less distinct bellies are present, providing tendons for toes I-IV (Bischoff, Deniker, Duvernoy, Hartmann, Hepburn, Owen, Pira, Sommer, No. 1105, No. 47). A tendon for the fifth toe was found in but one out of eight gorillas (Keith, 1899). The tendons for II-IV are prolonged, as in man, as parts of the extensor aponeuroses (Hepburn, Pira, No. 47). That to the hallux inserts on the base of the basal phalanx (Duvernoy, Hepburn, Pira, No. 47). Because of its transverse course toward the great toe, the inner belly becomes nearly a separate muscle.

The origin and insertions of this muscle in man are normally as in gorillas, and there are tendons for toes I-IV. A belly for the little toe may very rarely be present. Le Double cites instances in which only three tendons were present: for toes I-III, or for II-IV, or for I, III and IV, or for I, II and IV. Similarly he states that only two tendons, for I and IV, or for II and IV, may be found, or only one tendon, for III, or for IV. He also found the entire muscle absent in one foot of a cadaver which he dissected; the other foot was normal.

Other Primates show in general a similar origin for the muscle, with slight variations. Kohlbrugge notes that, in apes and monkeys, it may sometimes arise in part from other bones than the calcaneus (cuboid, cuneiforms, *naviculare*, and meta-

tarsals). Similar points of origin may occur in prosimians (Murie and Mivart).

In the chimpanzee there are usually four tendons, for I-IV, as in my specimen. A tendon for the fifth toe may, however, be present. According to Keith (1899), this occurred in four out of eleven animals. Tendons for I-IV were present in my orang. But the fifth toe may occasionally receive a tendon (Kohlbrugge). Similarly, in *Hylobates pileatus* I found tendons for I-IV, which is the rule for gibbons, but Kohlbrugge also found a tendon for V in *Symphalangus syndactylus*.

Old World monkeys have tendons for toes I-IV. This arrangement occurs, in *Papio sphinx*, *Lasiopyga* and *Pithecus* (Bischoff, 1870), in *Colobinae* (Kohlbrugge), in *Lasiopyga griseoviridis*, *Cercocebus aethiops* (*fuliginosus*), *Pithecus irus*, *Simia sylvanus* (*Inuus ecaudatus*), and *Papio cynocephalus* (Ribbing), and in *Pygathrix germaini* (Straus).

Similarly, in New World monkeys there are usually tendons for digits I-IV, as in *Pithecia monacha* and *Callithrix penicillata* (Bischoff), in *Brachyteles arachnoides*, *Cebus fatuellus* and *Callithrix jacchus* (Ribbing). But in *Ateles* the hallux may receive no tendon (Kohlbrugge).

The number of toes supplied by the short extensor varies greatly in prosimians. Murie and Mivart note the following arrangements: there are tendons for toes I-IV, as in most other Primates, in *Lemur catta* (right foot), *Galago crassicaudatus*, *G. alleni* and *Nycticebus coucang* (two bellies for toe IV in *Nycticebus*); for II-IV, the hallux receiving no tendon, in *Lemur catta* (left foot), *L. variegatus*, *L. nigrifrons* (left foot) and *Chiromys* (*Daubentonia*) *madagascariensis*; for I, II and III in *Daubentonia* (Owen's specimen); for I, II and V in *Lemur nigrifrons* (right foot); and for I and II in *Galago garnetti* and *Perodicticus*. The origin was partly from the fibula in *Lemur*

fulvus. In the specimens of *Daubentonia madagascariensis* studied by Zuckerkandl and by Oudemans, the hallux received no tendon, but those for toes II–IV were present in both instances. Ribbing found tendons for II and III in *Lemur mongoz*, for II–IV in *Lepidolemur*, and for I–IV in *Tarsius*. Ruge (1878a) found tendons to all five toes in *Loris tardigradus* (*gracilis*). Burmeister, Allen and Woollard found only tendons for I–III in *Tarsius*. In my galago there were tendons to all the toes, but only four muscle-bellies, the outermost belly giving off two tendons for IV and V.

In the highland gorilla (No. 47), there is, as I have already described, a fifth belly of the short extensor. This is very much smaller than any of the others. It arises between the bellies for toes I and II and its fibres are continuous with those of the second dorsal interosseus. Ruge (1878a) has described unions of the short extensor and the dorsal interossei in *Loris tardigradus* and the orang. He also studied (1878c) this union in man, in whom it occurs not too rarely. Such a union he regards as a progressive variation.

The phylogenetic history of the short extensor has been traced throughout mammals by Ruge (1878a). He believes that the entire muscle originally arose from the fibula, as he found it in Monotremes, and that there ensued a gradual migration to the dorsum of the foot, with a complete loss of the original peroneal relations. This migration began on the inner side of the foot, until, as in man, apes, and monkeys, the four inner bellies had attained a purely pedal origin. The occasional occurrence of a short extensor belly for the fifth toe, as he found in *Loris tardigradus*, would indicate a complete migration of all of the elements. The *peroneus digiti V* (which Ruge calls the *extensor brevis digiti V*), present in most mammals, he regards as the outermost tendon of the short ex-

tensor, which has retained its original position. It arises from the fibula and sends a slender tendon to toe V. This *peroneus digiti V* is normally absent in man, and in him, as in the anthropoids, according to Ruge, the muscle-belly has fused with that of the *peroneus brevis*.

The researches of Frets (1907, 1908, 1911), and those of Ribbing, have led these workers to disagree with the conclusions of Ruge. Frets believes that the *peroneus digiti V* cannot be regarded as the outlying portion of the *extensores breves*, for it may be present along with a short extensor belly for the fifth toe. He cites such cases in prosimians (1907). Likewise, a *peroneus digiti IV*, arising from the fibula, and going to toe IV, may also occur together with a short extensor belly for that toe. In my galago there was a *peroneus digiti V* and also a short extensor tendon for digit V. The latter did not, however, arise from a separate belly, but was of the nature of an accessory tendon from that which went to toe IV. Ribbing does not believe that the short extensor has wandered from the leg to the dorsum of the foot, but that it has always been a pedal muscle. It is needless to go into the details of his argument here, but I would state that he homologizes the mammalian short extensor with a pedal group of muscles found in other Tetrapods. The *peronei digiti IV* and *V* (which he calls *extensores laterales IV* and *V*) he regards as distinct from the short extensor group.

M. peroneus longus. Very few authors describe the insertion of this muscle in the gorilla. It is on the plantar surface of the base of the first metatarsal alone (Duvernoy, Hepburn), or on the first metatarsal and *cuneiforme I* (Pira), or on the first metatarsal and outer dorsal surface of the cuboid (No. 47). In No. 47 the metatarsal insertion was the primary one. In addition to these attachments, the ten-

don was attached by a tendinous plate in the peroneal sulcus of the cuboid. Chapman, Deniker, Owen and Sommer merely state that in their gorillas the muscle is as in man.

The *peroneus longus* normally inserts in man on the base of the first metatarsal, and also on the first cuneiform. It may sometimes also be inserted on the base of *metatarsale II*, or on *metatarsalia III* and *IV*, or on the tendon of the *tibialis posterior* (Le Double). The same author notes that the attachment may be confined to the hallucal metatarsal alone. Testut states that there may be a supernumerary insertion on *metatarsale V*.

In my chimpanzee the insertion of the muscle was limited to the base of *metatarsale I*. Bischoff (1870) and Hepburn found a similar attachment in their animals. A tendinous sheet may hold down the tendon in the peroneal sulcus (Straus).

I found the *peroneus longus* in the orang inserting on the base of the first metatarsal, but there was an additional insertion to the outer side of the cuboid, and the tendon was attached in the peroneal sulcus by a fibrous sheet. In other oranges the tendon may be limited to the base of the hallucal metatarsal (Bischoff, 1870; Hepburn), but a supernumerary insertion on the tuberosity of the fifth metatarsal is not very rare (Kohlbrugge).

In the gibbons the usual insertion is on *metatarsale I* alone (Bischoff, 1870; Hepburn; Kohlbrugge). But I found an additional small tendon to the base of *metatarsale V* and the cuboid in *Hylobates pileatus*.

The insertion in Old World monkeys may be limited to the base of the first metatarsal, as in *Papio sphinx*, *Lasiopyga* and *Pithecius* (Bischoff, 1870) and in *Colobinae* (Kohlbrugge), or the insertion may be chiefly on *metatarsale I*, with an accessory connection to the base of *metatarsale*

V, as in *Lasiopyga griseoviridis*, *Cercocebus aethiops*, *Pithecius irus*, *Simia sylvanus* and *Papio cynocephalus* (Ribbing) and in *Pygathrix germaini* (Straus). In my *P. germaini* the tendon was also bound down in the peroneal sulcus of the cuboid.

In New World monkeys the insertion may be confined to the base of *metatarsale I*, as in *Pithecius monacha* and *Callithrix penicillata* (Bischoff, 1870). Ribbing, on the other hand, found also an attachment to *metatarsale V* in *Brachyteles arachnoides*, *Cebus fatuellus* and *Callithrix jacchus*. This insertion was especially strong in *Callithrix*.

The *peroneus longus* insertion seems always to be confined to the base of the hallucal metatarsal in prosimians. Such an attachment was found in *Lemur catta* (Murie and Mivart), in *Daubentonia madagascariensis*, *Lemur variegatus*, *Galago crassicaudatus* and *Loris tardigradus* (Zuckerkandl), in *Lemur mongoz*, *Lepidolemur* and *Tarsius* (Ribbing), in *Tarsius* (Burmeister), in *Tarsius* (Allen), in *Tarsius* (Woollard), and in *Galago* (Straus).

In man a sesamoid cartilage or bone usually occurs in the tendon of the *peroneus longus*, where it curves around the outer border of the foot, in front of the tuberosity of the cuboid. No such sesamoid was present in my specimens of gorilla (No. 47), chimpanzee, orang, gibbon, and *Galago*, but the tendon was thickened at the point where the bone occurs in man. This thickening was especially marked in the orang and gibbon. In *Pygathrix germaini* I found a well-developed sesamoid bone at the usual position. Kohlbrugge found this sesamoid occurring, apparently constantly, in the *Colobinae* and the gibbons which he studied. It has been found in a chimpanzee by Wilder, by Pagenstecher in the drill, and in *Tarsius* by Woollard. Apparently this sesamoid has a rather haphazard occurrence.

Ruge (1878a) came to the conclusion that the *peroneus longus* primitively inserted on the lateral border of the foot (*metatarsale V*) and that its migration across the sole to the base of the first metatarsal was produced by its coming into closer relation with the plantar ligaments. This theory offers an explanation for the supernumerary insertions sometimes found in Primates, and which occur, among the anthropoids, most frequently in the orang. An attachment to the base of *metatarsale V*, or to the cuboid, as occurs in the *G. beringei*, would be regarded as a very primitive type of variation.

M. peroneus brevis. This muscle always shows, in gorillas, the same insertion as in man, on the base of the fifth metatarsal bone (Deniker, Duvernoy, Pira, Sommer, No. 1105, No. 47). It is to be inferred in the absence of detailed descriptions, that Bischoff, Chapman, Hepburn, Macalister and Owen found a similar attachment. All of these writers mention the muscle either as presenting the usual features, or as being as in man.

The prolongation of the *peroneus brevis* as a slender tendon to the fifth toe may occur in the gorilla and other anthropoids, and also in man. This tendon is in reality the terminal portion of the *peroneus digiti V*, and will be discussed with this muscle.

The variations of the *peroneus brevis* in man are of minor interest. They have been discussed by both Testut and Le Double. In my chimpanzee, orang, gibbon, *Pygathrix* and *Galago*, the muscle inserted on the base of *metatarsale V*. The digital prolongation was present in the first three, the complete *peroneus digiti V* in the last two.

The insertion of the *peroneus brevis* exhibits an astonishingly slight variability in Primates, being almost without exception on the base of the fifth metatarsal. Indeed, this would appear to be always the

arrangement in the anthropoids and in both Old and New World monkeys (Beattie, Kohlbrugge, Straus). *Metatarsale V* is also the point of insertion in most prosimians (Murie and Mivart, Milne Edwards and Grandidier, Zuckerkandl, Woollard, Straus). Only Burmeister found a different condition. In his *Tarsius* the tendon was inserted on the cuboid. Woollard, however, found it limited to the base of the fifth metatarsal in the same genus.

M. peroneus digiti V (fig. 27). This muscle, or its vestiges, has been described under various names, some of which follow: *peroneus medius* (Cuvier), *peroneus parvus* (Bischoff), *peroneus accessorius* (Henle), *extensor brevis digiti V* (Ruge), *extensor lateralis digiti V* (Ribbing). It is not known to occur as a distinct muscle in the gorilla. It may exist, however, in a vestigial condition. In such instances the terminal portion of the tendon alone is present, associated with the tendon of the *peroneus brevis*. The latter, just prior to its insertion on the base of *metatarsale V*, gives off a narrow prolongation to the fifth toe. It is unnecessary to discuss the reasons for regarding this accessory tendon of the *peroneus brevis* as the vestige of the *peroneus digiti V*, but they are most logical (see papers by Frets). Such a vestigial *peroneus digiti V* has been found in the gorillas of Deniker (both fetus and juvenile), Macalister and Pira. It also occurred in No. 47, the tendon of the *peroneus tertius* being split to allow its passage. In the left foot of No. 47 Morton found a similar tendon, but here it was as a prolongation of the *peroneus tertius*, and not of the *peroneus brevis*. The tendon to the fifth toe which he describes and figures in his young lowland gorilla, and which also was associated with the *peroneus tertius*, is likewise very possibly a remnant of the *peroneus digiti V*. No traces of a *peroneus*

digiti V were found in the gorillas of Bischoff, Hepburn, Ranke, Rothsuh and Sommer. It also was probably absent in the animals studied by Chapman, Duvernoy, Hartmann and Owen, all of whom neither mention nor figure it, although they all discuss the other peroneal muscles. Unfortunately, I have no note of its occurrence or absence in No. 1105. As to its percentage frequency, it has been found, always in a vestigial form, in 35.7 per cent (5 out of 14) of gorillas.

In man the digital prolongation of the *peroneus brevis* tendon is not infrequently present. Le Double found it in 34 per cent (34 out of 100) of Europeans, Wood (cited by Le Double) in 35.3 per cent (36 out of

The end portion of the *peroneus digiti V* tendon is present as an extension of the *peroneus brevis* tendon in some chimpanzees, orangs and gibbons. As already stated, I found it occurring in my specimens of these animals. In the orang it failed, however, to reach the fifth digit, the weak tendon thinning out into the fascia over the dorsum of the outermost metatarsal.

The *peroneus digiti V* is not, however, always represented in these animals. For example, it has been found in the chimpanzee by Brühl, Champneys, Fick (in three animals, 1925), Hartmann, Humphry, Macalister, Wilder and myself, but not by Bischoff (1870), Hepburn, Michaelis, Ranke, and Rothsuh; in the

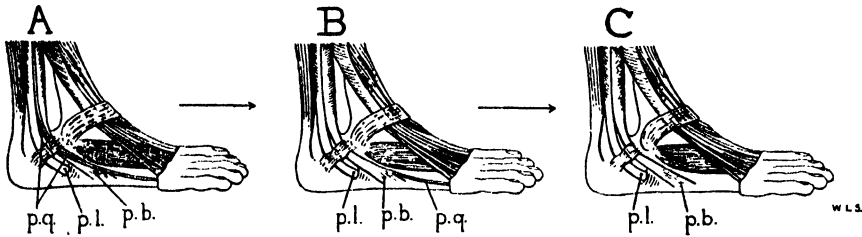


FIG. 27. STAGES IN THE PHYLOGENETIC REDUCTION OF THE PERONEUS DIGITI V MUSCLE IN PRIMATES

A. Complete muscle, arising from fibula. B. Reduction to a prolongation of the peroneus brevis tendon. C. Complete disappearance. *p. q.* = peroneus digiti V; *p. b.* = peroneus brevis; *p. l.* = peroneus longus.

102),—a frequency practically equal to that in the gorilla. The complete muscle itself may also rarely occur in man (Le Double). Probably the so-called *peroneus quartus* of Otto, arising from the fibula, but which does not reach the fifth toe, and which may sometimes be found in man, is merely a *peroneus digiti V* in which the muscle-belly and proximal portion of the tendon are well-developed, while the terminal portion has become vestigial or disappeared altogether. This would seem to be the view of Frets (1907, 1911) also. He describes what is apparently a typical *peroneus quartus* occurring in the same body with a digital prolongation of the *peroneus brevis* (1911).

orang by Fick (1895), Frets (1907), Hepburn, Langer, Michaelis and myself, but not by Bischoff (1870), Ranke, Rothsuh and Ruge (1878a); and in the gibbon by Chudzinski (cited by Sommer), Kohlbrugge (in *Hylobates agilis* and *H. leuciscus*) and myself, but not by Bischoff (1870), Hepburn, Kohlbrugge (*Symphalangus syndactylus*), Ranke (2 animals) and Rothsuh. In the orangs of Fick, Frets, Michaelis and Langer, and in the *Hylobates leuciscus* of Kohlbrugge, the complete muscle, arising from the fibula, but in various degrees of development, was present. In all the others there occurred only the terminal portion of the tendon, prolonged from that of the *peroneus brevis*, and

in some instances failing to reach the fifth toe.

In both groups of monkeys and in prosimians a complete *peroneus digiti V* is nearly always present (Beattie; Bischoff, 1870; Burmeister; Frets; Kohlbrugge; Murie and Mivart; Ranke; Ribbing; Wool-lard; Zuckerkandl; Straus). It may, however, occasionally be absent, as in *Papio cynocephalus* (*Cynocephalus babuin*) (Michaelis), and in *Daubentonia* (*Chiromys*) *madagascariensis* (Owen, cited by Murie and Mivart and by Zuckerkandl). It arises from the fibula in more or less close association with the *peroneus brevis*, and the tendons of the two muscles may be contained in a common sheath, as I found in *Pygathrix germaini*.

Normally its tendon goes to the dorsal aponeurosis of the fifth toe. In Kohlbrugge's *Nasalis larvatus* the insertion was anomalously on the tuberosity of the fifth metatarsal bone. For a most complete account of this muscle in various Primates, the reader is referred to the papers of Frets.

M. peroneus digiti IV. I have found no record of this muscle in anthropoid apes. It occurs rather regularly in prosimians (various authors), and in some monkeys (Frets, Ribbing). In both lower extremities of a human embryo, Ribbing found a well-developed muscle arising on the outer side of the *peroneus brevis*, from the lower portion of the fibula. In the left foot it inserted on the calcaneus; in the right, on *metatarsale V*. Ribbing regards this as homologous with the *peroneus digiti IV* (his *extensor lateralis digiti IV*) of other Primates. It is, more likely, however, nothing more than a *peroneus quartus*, which sometimes occurs in man. This *peroneus quartus*, as previously stated, in all likelihood represents the more proximal portions of the *peroneus digiti V*, and probably has no relation to a true *peroneus digiti IV*.

Nerves. The arrangement and distribution of the nerves in the foot of my highland gorilla (No. 47) is like that of the lowland gorilla (Eisler, 1890; Hepburn; Sommer). In turn, the latter animal agrees with the conditions found in man. The pedal nerves have been but rarely described in the gorilla. The most detailed account is apparently that of Eisler. I have not, however, had access to his article. Those of his findings to which I shall refer have been gleaned from the writings of Kohlbrugge. Hepburn gives a rather full description of the distribution of the nerves in his specimen, while Sommer notes the innervation of the various muscles. The innervation of the *flexor digitorum brevis* is given by Sawalischin for her two gorillas. A passing comment on the plantar nerves is made by Chapman. He merely states that "in a similar manner to that of man, the plantar nerves furnish the nervous supply to the foot of the Gorilla."

The courses of the nerves in Hepburn's animal and in No. 47 agree exactly with the usual arrangement in man. As to the nerve-supply of the individual muscles, in table 4 I have arranged the findings of Eisler, Hepburn and Sommer for comparison with the conditions in No. 47. I have not considered the purely cutaneous branches. It will be noted that the innervation of the muscles varies only in those cases in which variability is encountered in man. Thus, the *lumbricales* show an instability in their nerve-supply. That for toe II is always supplied by the medial plantar nerve, and that for V always by the lateral plantar. The two intermediate *lumbricales* may be innervated by either plantar nerve. The *flexor digitorum brevis* may receive its supply from the medial plantar nerve alone (Hepburn, Sommer, both specimens of Sawalischin, No. 47?), but it may also have a branch from the

lateral pl., as in Eisler's animal. The *flexor digiti V brevis* (and the *opponens digiti V*, when present) and the interosseous muscles of the fourth space are always, as in man, supplied by the lateral plantar nerve, but the fibres to these

flexor hallucis brevis, or at least a portion of its anlagen, had fused with the adductor. Hence the double nerve-supply.

Kohlbrugge has summarized and discussed the nerves of the foot in other Primates. These possess the same arrange-

TABLE 4
Innervation of the separate pedal muscles in various specimens of gorillas

	NO. 47	HEPBURN	SOMMER	EISLER
<i>Abd. ball.</i>	Med. pl.	Med. pl.	?	
<i>Abd. dig. V</i>	Lat. pl.	Lat. pl.	Lat. pl.	Lat. pl.
<i>Abd. oss. met. V</i>	Lat. pl. (?)	Lat. pl. (?)	Lat. pl.	
<i>Fl. dig. brev. (superf.)</i>	Med. pl.	Med. pl.	Med. pl.	Med. pl. et lat. pl.
<i>Fl. dig. brev. (deep)</i>	?		Med. pl.	
<i>Lumbrical II</i>	Med. pl.	Med. pl.	?	Med. pl.
<i>Lumbrical III</i>	Med. pl.	Lat. pl. prof.	?	Med. pl.
<i>Lumbrical IV</i>	Med. pl.	Lat. pl. prof.	?	Lat. pl. prof.
<i>Lumbrical V</i>	Lat. pl. superf.	Lat. pl. prof.	?	Lat. pl. prof.
<i>Quad. plant.</i>		Lat. pl.		
<i>Fl. ball. br. (fib.)</i>	Med. pl.	Med. pl.	Med. pl.	
<i>Fl. ball. br. (fib.)</i>	Med. pl.	Med. pl.		
<i>Opponens ball.</i>	Med. pl.	Med. pl.		
<i>Add. ball.</i>	Lat. pl. prof.	Lat. pl. prof.	Lat. pl. prof.	Lat. pl. et med. pl.
<i>Fl. dig. V brev.</i>	Lat. pl. prof.	Lat. pl. superf.	Lat. pl.	Lat. pl. prof.
<i>Opp. dig. V</i>		Lat. pl. superf.	Lat. pl.	
<i>Int. plant.</i>	Lat. pl. prof.	Lat. pl. prof. et superf.	?	Lat. pl. prof.
<i>Int. dors.</i>	Lat. pl. prof.	Lat. pl. prof. et superf.	?	Lat. pl. prof.
<i>Fl. fibularis</i>	?	Tib.	Tib.	
<i>Fl. tibialis</i>	?	Tib.	Tib.	
<i>Tib. post.</i>	?	Tib.	Tib.	
<i>Exts. ball. et dig. brev.</i>	Per. prof.	Per. prof. (?)	?	
<i>Ext. ball. long.</i>	?	Per. prof. (?)	Per. prof.	
<i>Ext. dig. long.</i>	?	Per. prof. (?)	Per. prof.	
<i>Per. tertius</i>	?		Per. prof.	
<i>Tib. ant.</i>	?	Per. prof. (?)	Per. prof.	
<i>Per. long.</i>	?	?	Per. superf.	
<i>Per. brev.</i>	?	?	Per. superf.	

muscles may be carried by either the superficial or the deep branch of the nerve. The superficial branch of the lateral plantar nerve may contain no motor fibres, as in Eisler's specimen. All of the above-cited variations also occur in man. Eisler found both plantar nerves supplying the *adductor hallucis*. Possibly the fibular head of the

muscles as do gorilla and man, and the same variations.

CONCLUSIONS

The foot musculature of the lone specimen of the highland gorilla, *G. beringei*, falls, in practically all its details, well within the range of variation exhibited by

the known examples of the lowland gorilla, *G. gorilla*. The most striking difference lies in the arrangement of the long flexors, but, as I have pointed out, this should be regarded as a variation of exceedingly primitive pattern. Certainly it can hardly be viewed as a peculiarity of the highland species; at least, not until more highland gorillas have been dissected, and until further lowland gorilla feet are thoroughly studied. Similarly, the accessory attachment of the *peroneus longus* tendon to the outer border of the foot falls in the category of atavistic variations. Possibly the little muscle of the deepest plantar layer, which yokes the second and third toes, and which occurs only in the two *G. beringei*, will eventually be found to be a peculiarity of this species. But in this, as in other points, we cannot be certain until more examples of both species, and particularly of *G. beringei*, have been carefully studied.

If it is finally shown that the foot musculature does differ in the two forms, I think it safe to predict that such a difference will only be an average one. Keith (1899) has shown that this is largely true in respect to the differences in the foot muscles of the gorilla and the chimpanzee. We can therefore hardly expect any striking differences between the two gorilla species.

The foot musculature of the gorilla makes a closer average approach to that of man than does the foot musculature of the chimpanzee. This seems most likely to be a convergence caused by the habits of the gorilla, and is not to be regarded as indicating a closer genetic relationship to man. Whereas the chimpanzee is essentially an arboreal animal, the adult gorilla, probably at least in part because of its huge size, has become almost wholly terrestrial. Such a change in mode of life has led to convergences towards the human form, none of which are more striking

than in the foot. But even so the general plan of the gorilla foot is essentially that of an arboreal Primate, and in some respects it is highly specialized in a different direction than that of man. The orang, on the other hand, has become very highly adapted to a purely arboreal life, and in consequence has undergone certain specializations peculiar to itself. Naturally the foot shows changes, not only in the skeleton, but also in the muscles, e.g., the complete elimination of the long hallucal flexor tendon and the development of an *opponens hallucis*. These specializations are almost certainly associated with the reduction of the great toe in the orang. In most characters of the foot the orang is further removed from man than are the chimpanzee and the gorilla, in a few it is closer. On the whole it is highly specialized in its own direction. The gibbon foot is intermediate between the typical Old World monkey foot and those of the great apes. In some characters, as in the flexor muscles, it is more like the monkeys; in others, as in the deep plantar muscles, it is more like the great apes. The general plan of the foot musculature of both Old and New World monkeys is more primitive than that of the anthropoids and man. The typical prosimian foot is in some characters like that of the typical monkey, in others more primitive, and in still others extremely specialized in its own direction. The prosimian foot thus in no sense stands in linear relationship to those of other Primates, but is in general a structure specialized along its own lines.

The reader has probably already noted that in some of the foot muscles there exist, on the whole, but little if any differences among Primates. These muscles are to be regarded as very primitive and conservative in their structure, and hence can yield but little evidence in any study of the evolution of the Primate foot.

Certain groups of muscles, however, show a wide range of variability and differ markedly among the various Primate groups. Such muscles are the long and short flexors of the toes, the deep plantar muscles, and to a less extent the peroneal group. A thorough study of these will reveal the important changes which have taken place in the Primate foot.

In conclusion, I would again state that,

in its musculature, as in its skeleton and outer form, the foot of the gorilla more closely approaches that of man than does the foot of any other Primate. But at the present time it is very difficult to decide which of these similarities are indications of close genetic relationship, and which are merely due to convergence produced by interaction of environmental forces and an ancient, basic ground plan.

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THE HYDROGEN-ACTIVATING ENZYMES OF THE CELLS

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Lund, Sweden

I. HEINRICH WIELAND'S NEW CONCEPTION OF CERTAIN OXIDATION PROCESSES

H EINRICH WIELAND, of Munich, the celebrated chemist who in 1928 was awarded the Nobel prize, must be considered as the discoverer of the enzyme group called the dehydrases or dehydrogenases, characterised by their power to activate the hydrogen of certain organic substances so that it will be able to cause reactions, not occurring in the absence of these enzymes.

Of the two terms dehydrases and dehydrogenases, I prefer the latter, for which I myself am responsible. It seems to me that when translated into various languages this term will give rise to fewer mistakes or misunderstandings than any other. The designation "dehydrases" has the advantage of being shorter, it is true, but it may in certain languages easily be taken to mean an enzyme which deprives the substance, not of hydrogen, but of water. This misunderstanding of this scientific term would be natural also on account of the fact that in technical language a substance deprived of water is said to be dehydrated.

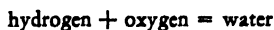
The name "redoxases" has also been suggested for these enzymes, by von Euler, Jr. The name is short and is based on the fact that oxidations and reductions are bound up with each other. Any oxidation of one substance implies reduction of something else. To take the simplest in-

stance, when oxygen and hydrogen unite we may speak of the oxidation of the hydrogen to form water, or of the reduction of the oxygen, also to form water. Every oxidase is certainly a reductase and it is quite legitimate to express this fact by means of such a name as redoxase. But in objection to this designation "redoxases" for the group of enzymes which I prefer to call "dehydrogenases," it may be pointed out that the name "redoxases" seems to suggest a wider group of enzymes than intended. It would apply to the enzymes transporting oxygen just as well as to those transporting hydrogen. That is to say, the designation is too wide for the group it is meant to refer to.

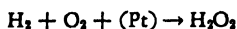
Still another name has been proposed, the name "hydrogeno-transportases." I am responsible for this name also. It was suggested for and seems to me to fit particularly those processes which are reversible and characterized by a mutual interchange of hydrogen between two substances and which processes occur under the influence of these enzymes.

In 1912 and 1913 Wieland published a new conception of the mechanism of the oxidation of certain inorganic and organic dysoxidisable substances at low temperatures and without help of such very active agents as strong acids or alkalis. According to his theory the oxidation is due to the activation of the hydrogen of the substances, not as was thought before to an activation of oxygen.

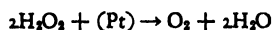
The oxidation theory of Wieland was at first developed in the field of pure chemistry. The simplest example of an oxidation in which we seem to have to assume the activation of hydrogen to be the main factor is the reaction:



Pure hydrogen and oxygen do not react with each other with a measurable velocity at lower temperatures. But in the presence of spongy platinum or palladium they do.



Then the hydrogen peroxide is split up into water and oxygen, this process being also catalyzed by the platinum:



Earlier, it was believed that this reaction was due to an activation of oxygen with formation of a peroxide of the metal as an intermediary stage. Since, however, hydrogen peroxide has been shown to be the intermediate oxidation product it seems more probable that the hydrogen has been activated, and that the oxygen molecule plays the part of an "acceptor" for the hydrogen activated.

That the hydrogen is activated is demonstrated by the fact that oxygen as hydrogen acceptor can be replaced by other substances, e.g. methylene blue. Methylene blue, (=Mb.) a quinoid dye stuff with no oxygen in the molecule, is reduced by activated hydrogen to colorless leuco-methylene blue.

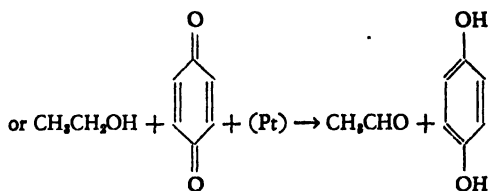
When one bubbles hydrogen through a solution of Mb. no reduction to leuco-Mb. will take place, but if one also adds some spongy platinum the blue color will soon disappear. The hydrogen has been activated and reacts with the dye stuff to form leuco-Mb.

In this case we had to do with an activation of free hydrogen. But bound hydrogen can also be activated in the same way. Let us take the following example: For a long time it has been known that primary alcohols will be oxidized to aldehydes by oxygen in the presence of spongy platinum



(In the same way as in the last example H_2O_2 is an intermediary oxidation product.)

In this case also there is an activation of hydrogen. The oxygen has the function of a hydrogen acceptor, which can be replaced, for example, by Mb. or quinone.



As early as 1913 Wieland extended his theory to embrace also certain biological oxidation processes. In that year he was able to show that the acetic acid bacteria are able to oxidise alcohol to acetic acid even in the absence of oxygen, if only a suitable hydrogen acceptor, e.g. Mb. is present. The alcohol is changed into acetic acid and the Mb. is transformed into its leuco-form, which shows that what is called oxidation of the alcohol is in reality a dehydrogenation.

Wieland did not succeed in extracting in soluble form the enzymes, which may be supposed to cause the action of the bacteria on the alcohol.

If we keep up the distinction between, on one hand, pure enzymatic effects and, on the other, protoplasmatic effects depending on the protoplasm structure, Wieland must

be said to have shown that the acetic acid fermentation must be regarded as a dehydrogenation; but at the same time we lack full evidence that this dehydrogenation is effected by enzymes. It might possibly be due to other resources of the protoplasm.

For my own part I may say, that I don't believe much in such a distinction. It is at any rate certain, that this objection does not apply to the mechanism of another biological process, which Wieland investigated in connection with the one mentioned above: viz. the so-called Schardinger reaction.

Fresh milk will not reduce Mb. and if formaldehyde (or some other aldehyde) is added to milk, it remains for long without change. But when both formaldehyde and Mb. are added (and especially, if oxygen is excluded) the Mb. is reduced to the leuco-compound, while the aldehyde is oxidised to formic acid. Boiled milk does not show the reaction, because the enzyme has been destroyed.

Now Wieland was able to show, that in the case of this reaction the aldehyde functions as a "hydrogen donator," if we use the term I later introduced. The hydrogen of the aldehyde or to be more precise, the hydrogen of the hydrate form of the aldehyde, not of the aldehyde itself, is activated by the Schardinger enzyme and this activated hydrogen reacts with the Mb. which is transformed to leuco-Mb. By giving off this hydrogen the aldehyde hydrate is simultaneously transformed to the corresponding acid.

It ought to be mentioned, that a few years earlier Bredig had already interpreted the Schardinger reaction in a similar way. In a paper "Die Schardingersche Reaction und ähnliche enzymartige Katalysen" Bredig and his collaborator Sommer wrote as follows:

Thus we have found that the inorganic catalysts as well as the milk enzyme very easily transport the oxygen of the methylene blue to oxidisable substances as e.g. formaldehyde. Or, to be more exact, they transport the hydrogen of the formaldehyde to reducible substances such as the dye mentioned above. In reality it is surprising to find there exists a high degree of resemblance between the inorganic catalyst and the milk enzyme in this Schardinger reaction.

At the same time it must be pointed out, in fairness to Wieland, that Bredig never experimented on the real biological enzyme; he pointed out an interesting analogy based on the result of inorganic model experiments and gave a successful interpretation of it. Wieland, on the other hand, worked on the biological enzyme and showed how it was possible for the aldehyde while it functioned in its hydrate form to serve as a source of hydrogen by the decolorisation of Mb.

2. THE APPLICATION OF THE IDEAS OF WIELAND TO THE PROBLEM OF THE OXIDATION OF "METABOLITES" OF HIGHER ORGANISMS. THE "SUCCINO-DEHYDROGENASE"

The examples of biological dehydrogenation brought forth by Wieland concerned bacteria and an extra-cellular enzyme which at that time seemed to be of no great account in the metabolism. The importance of Wieland's ideas for the understanding of the intracellular oxidation processes of higher organisms was first shown by the discovery of other dehydrogenases, able to activate substances, which undoubtedly had a place in the metabolism of the higher organisms e.g. succinic acid, malic acid, citric acid, lactic acid, and glutamic acid.

Of these enzymes it is primarily that acting on succinic acid, i.e., the "succino-dehydrogenase," which has served to bring out characteristics of the group. Some words may be said about its detection.

A quarter of a century ago I began a

series of investigations concerning the respiration of the isolated muscle in its dependence on various factors. Using an apparatus which I had constructed for this purpose, the micro-respirometer, I studied the respiration not only of the intact muscle but also of minced muscle substance. I investigated how the respiration of such muscle substance was influenced by various substances, e.g. the fatty acids and their derivatives.

During the course of these studies I found in 1909 that the oxygen consumption of the muscle substance was increased by the neutral alkali salts of succinic acid.

On the basis of this observation of mine Battelli and Stern, of Geneva, showed that the increase of oxygen consumption, which is caused by succinic acid, corresponds to one atom oxygen per molecule succinic acid. The next step was the discovery by Einbeck that the succinic acid is oxidised by the muscle substance to fumaric acid. The reaction mixture shows also a content of malic acid, which seems to have been formed from the fumaric acid under the influence of a hydrolytic enzyme, discovered by Battelli and Stern and called by them "fumarase". The investigations of Dakin have thrown further light on the nature of this reaction and shown that the malic acid, which is formed from the fumaric acid, is the laevo-form. We have also to thank Dakin for our knowledge of the quantitative conditions in the equilibrium between fumaric acid and malic acid.

However, before the processes in question had been investigated up to this point, the continuation of my own experiments had led to some new results.

The observation that succinic acid is very easily changed into fumaric acid under the influence of animal tissues, was bound to cause surprise. The succinic acid represents the final stage of the oxidation of fatty acids with such an agent as e.g.

nitric acid, which means that the succinic acid itself is resistant against these strong oxidation agents. During my attempts to find the explanation why in spite of this fact succinic acid is so easily oxidised in the organism, I came across Wieland's accounts of his investigations referred to above. They seemed to me to furnish a possibility for the explanation I wanted, and as a working hypothesis I postulated that the oxidation of succinic acid in the tissues is made possible by the activation of its hydrogen.

In order to verify this I made the following experiment. In each of two tubes, which could be evacuated, I placed equal quantities of muscle substance and of Mb. In one of the tubes I further placed some succinic acid in the form of its neutral potassium salt. The tubes were then evacuated and placed in a thermostat at 35°C.

The two tubes behaved quite differently. The tube which did not contain succinic acid showed no change in its color, while the mixture in the other tube soon had been wholly decolorised.

Since the Mb.-decoloration requires the presence of activated hydrogen this result fully proved that succinic acid under the influence of the enzymes of the muscle tissues is activated in regard to its hydrogen. The only reaction product which can very well be imagined to occur under these circumstances is fumaric acid.

Afterwards several investigators have proved by direct analysis that fumaric acid is formed from succinic acid by the influence of the dehydrogenases in spite of the absence of oxygen if only a suitable other hydrogen acceptor is present (Quastel & Wetham, using bacteria, 1924; Gottwalt Fischer, using muscle substance, 1927; and Hahn & Haarmann, also using muscle substance, 1927).

Having found that the oxidation of such a substance as succinic acid by animal tis-

sues is begun by an activation of its hydrogen, I went on to investigate if, or to what extent, a similar mechanism played a part in the oxidation of a certain number of other substances, and how the hydrogen-activating power of the cells and their enzymes was influenced by various factors.

The field of the investigations planned was wide and in order to make it possible to cover it in available time I first elaborated a convenient and handy method. The method is now used in many other laboratories than my own. I think it was the Cambridge school, which gave it the name "The Thunberg technique."

3. THE "THUNBERG TECHNIQUE"

The most important constituents of the Thunberg technique are the vacuum test tubes. "Thunberg-tubes" serve while keeping out oxygen to contain the reaction mixture, in which the hydrogen activation is going on, and in which also an indicator for activated hydrogen is present. Keeping out the oxygen is necessary for two reasons. If oxygen is present it may work as a hydrogen acceptor. The active hydrogen divides then between the oxygen and the indicator according to unknown laws, the reaction velocities and the affinities being the deciding factors. Other factors are the concentrations of the two acceptors, which concentrations vary during the course of the experiment. By keeping the oxygen absent the undesirable accessory reaction with this substance is eliminated. The total quantity of hydrogen formed during the reaction in that way is taken over by the indicator and kept by it.

Only when the experiment is carried out in the absence of oxygen is it practicable to use as indicator substances, e.g. methylene blue, the reduction forms of which are oxidised by oxygen.

A Thunberg tube is a glass tube usually

holding about 10 cubic centimeters, one end of which is closed, while the other is open. The open end can be closed by means of a stopper of conical form and fitting very closely. A hole in the stopper can be made to communicate with a side-tube closed by turning the stopper. This side-tube can by a rubber-tube be put into communication with a vacuum pump.

In order to prevent air or water from penetrating into the vacuum tube after its evacuation it is necessary to treat the stopper with a good vacuum grease. [3 parts *Adeps lanae* (= dehydrated lanolin), 2 parts *Vaselinum* and 3 parts Bees wax are melted together and stirred during the cooling, so that a homogeneous grease is obtained.]

After the evacuation the vacuum tube is placed under water in a thermostat. One side of this thermostat is made of glass so that it is possible to observe the vacuum tubes. The other parts of the inside of the thermostat are painted white in order to facilitate the observation of the color changes of the vacuum tubes.

The temperature of the thermostat is kept constant within a range of 0.1°C. by a good thermo-regulator (e.g. an Ostwald toluol regulator).

The vacuum tubes must be protected against too strong light since otherwise the decoloration would be accelerated. Precautions must be taken so that some tubes are not subjected to stronger light than others. The thermostat is best placed in a fairly dark corner of the room, a special lamp being lighted for the moment of observation.

As indicator on the activated hydrogen different substances can be used. Methylene blue has been used more extensively than any other. A few words about this substance may therefore be said.

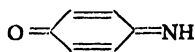
This valuable dye was discovered by Caro in 1876 and has since then been widely

used in the dye industry. As early as 1885 Dreser introduced it in the biological technique for certain biological reaction processes. Wieland utilized it in his first experiments in 1913 with the dehydrogenases and since then it has been constantly used for these studies.

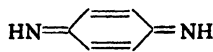
Mb. is a compound free from oxygen and formed by two six-membered rings of carbon atoms bound together by a six-membered ring containing one nitrogen atom

group belong e.g. the thiazins. The quinone-imid part of the molecule is of greatest account for the dye character of these substances. That their tendency to act as dyes is actualized is due to the entrance in the molecule of what is called auxochromatic groups. The NH_2 group functions as such in the thionin and its derivatives, e.g. Mb.

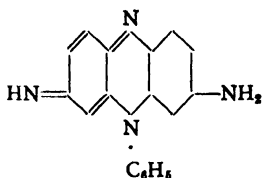
A point of interest is the question of what changes take place in the Mb. mole-



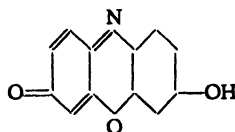
Chinon-monimid



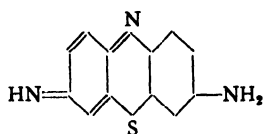
Chinon-diimid



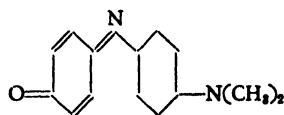
Phenosafranin



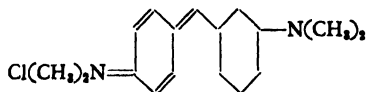
Resorufin



Thionin



Phenolblau



Dimethyl-phenylengrün

and one sulphur atom. It belongs to the group of the thiazin substances and may be regarded as a derivative from another well-known dye, Lauth's violet, or thionin. Mb. is tetra methyl thionin.

Mb. belongs to the very wide group of dyes, which all may be characterized as quinonimid dyes. Certain of these have their imid group acyclically bound, e.g. the indophenols and indamins. To the compounds with a cyclically bound imid-

cule when, under the influence of a reducing agent, it is changed to its leuco-form. Generally this reaction is expressed in the following simple way:



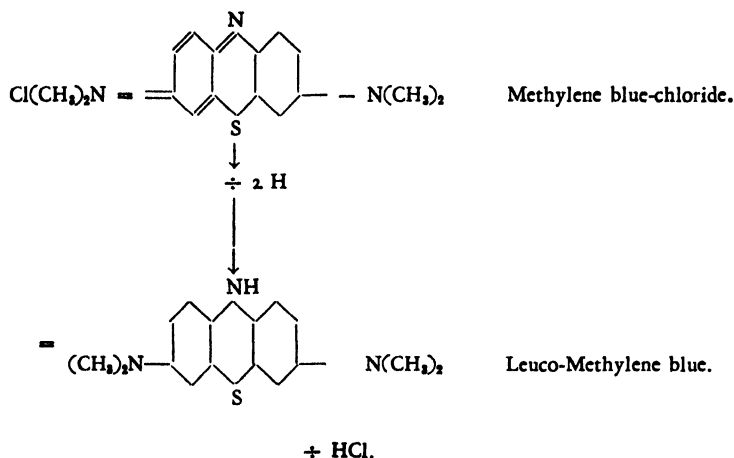
This equation is permissible for some practical purposes but is open to the objection that it will easily cause misunderstandings. It must not be taken to mean that the ring structure remains unchanged

when Mb. is reduced. As a matter of fact the quinoid binding with its two double bonds is changed to a benzoid binding. Since the dye character depended on the quinoid binding it is obvious that in this way the substance must be decolorized.

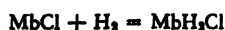
The equation given above seems to express the introduction of two hydrogen atoms in the Mb. molecule. This needs to be explained.

When speaking of Mb. experiments we mean in reality experiments with some

the formation of a chloride, this is not the case with the leuco-Mb. molecule. But it may on the other hand possibly give rise to a hydrochloride. This hydrochloride of leuco-Mb. will however rapidly and to a great extent dissociate giving off hydrochloric acid with change of the 5-valent nitrogen to 3-valent. Thus, if Mb. is reduced—for which reduction two atoms of hydrogen are necessary—we obtain one molecule Mb.H and in addition one molecule free hydrochloric acid. Notwithstanding the different final fates of the two



Mb. salt usually the Mb. chloride. There is no need to discuss here how the Mb. chloride is transformed in the phosphate solution used for dehydrogenase experiments. It seems likely that Mb. appears as an ion both in the pure water solution of its chloride and in the phosphate solution. In any case the chemical equation expressing the transformation of Mb. under the influence of reducing agents can be based on the salt formula. The more simple formula given above will then appear in the following form:



It may be objected that although the constitution of the Mb. molecule allows

H-atoms in question, we may very well use the short formula given above, since we are entitled to assume that the leuco-Mb.-HCl appears at least as a transitory product.

Mb. is available either as a chloride or as a zinc double chloride. Only the chloride is to be used as indicator. Not a few mistakes are probably to be put down to the unintentional use of the zinc double chloride.

Mb. is easily dissolved in cold water. Even in the case of dilute solutions, as 1:5000 or 1:1000, Mb. dissolves only slowly, and on account of this the solution ought to stand at least one day before being used.

The leuco-Mb. (= LMb.) is not so soluble as Mb. In acids LMb. is soluble to about 0.5 millimolar (= 1:5000), and in alkaline solutions to about 0.02 millimolar (= 1:125000). By reduction of a concentrated solution of Mb. the resulting LMb. gives a precipitate. If this fact is unknown to the experimenter he very easily puts a false interpretation on the precipitate formed in the reaction mixture during an experiment.

Before starting a series of experiments it is a good plan to make ready 100 cc. of the various concentrations 1:500, 1:1000, 1:1500, 1:5000, and 1:10000. The solutions must be kept in the dark. They will keep for months. The apparently great adsorption on the glass of the bottle is of no account. It may be due to the formation of some Mb-Silicate.

4. THE GENERAL DEHYDROGENASE-SYSTEM OF THE ANIMAL TISSUES

With this method I began in 1917 a series of investigations of the dehydrogenases of animal tissues. During my experiments with my micro-respirometer I had found that the oxygen consumption of the surviving, perfectly fresh frog muscle substance was strongly increased under the influence of malic acid, fumaric acid, and citric acid. I now began to investigate whether the hydrogen of these substances is activated, when they are added to muscle substance in vacuo.

Such fresh muscle substance already possesses a strong decolorisation power independent of every extra addition of donator substance, which decoloration obviously must be due to donator substances already present in the system. This spontaneous decoloration makes it often difficult to observe a possible decoloration-effect caused by the addition of other donator substances.

In order to avoid this difficulty I extracted the fresh muscle substance with water, or some suitable salt solution, and thus, by depriving it of at least the greatest part of its preexisting donators which is possible without extracting the enzymes at least to the same degree, brought the spontaneous decoloration down to a minimum of no importance. I then used this extracted muscle substance for the investigation of the substances mentioned above and of a great number of other substances.

The results of these experiments showed that the before-mentioned three substances: malic acid, fumaric acid, and citric acid, possess a strong power to cause the decoloration of Mb. in vacuo, if they are influenced by muscle substance. Thus it is clear also in the case of these acids that their oxidation by the tissues is begun by the activation of their hydrogen.

Among the considerable number of other substances investigated I found a considerable power of reducing Mb. in vacuo under the influence of animal tissues in the case of the following acids: lactic acid, α - and β -oxybutyric acid, l-tartaric acid, mesotartaric acid, α -oxyglutaric acid, and glutamic acid.

In my analysis of these facts and especially of the catalytic factors in question I wrote as follows (For reasons given below I will give here a word for word translation of this part of my paper.):

The reduction processes which have thus been discovered are in all probability of enzymatic nature.

It is obvious, to begin with, that for these processes some compounds of the cell are necessary. If the salts of the above-mentioned organic acids are mixed only with Mb., no decoloration process takes place. This only happens when tissue substance is added to the mixture. In order for such decoloration to take place the tissue substance washed in the way previously described is insufficient.

The necessary factors are: 1. the presence of one factor in the cell substance, 2. the donator substance,

3. Mb. or some other acceptor susceptible to hydrogen. Thus the reaction is obviously bound to what may be termed a chemical three-compound system, or, to be precise, a catalytic three-compound system.

Somebody might ask whether the supposition of such a three-compound system does not mean a simplification of the actual conditions. More components than suggested by this name might be necessary for the reaction. Further, is not the necessary cellular factor of so complicated a nature that it cannot be called an enzyme but must be looked upon as belonging to the normal cell-structure.

However, what the cell structure seems to be able to effect in preference to a simple physical-chemical system, is a harmonic course of the continuous links of a long reaction chain, and, further, the transformation of chemical energy into other forms of energy, e.g. mechanical energy (*via* surface tension changes or imbibition changes), electrical energy, osmotic energy, etc. But there is no reason to suppose that in order to take place a simple chemical process would require the presence of a cellular structure. The deleterious conditions to which muscle mass has been subjected speak against the supposed importance of the cell structure to the reactions in question. The mincing of the muscle cells and the treatment with distilled water are factors which must derange the polyphasic system of the muscle cells, i.e. their structure.

Thus there is every reason to suppose that these decoloration phenomena are vital not in the sense that they demand the preservation of the cell structure but only in that they require the presence of the enzymes active in the cells. Conceded that these processes are of enzymatic nature, the question will be: have we here a single enzyme with general effect or are there many enzymes, each with its specific effect?

In one respect there is no doubt about the answer. The succino-dehydrogenase must be a specific enzyme. On account of its great resistance it can easily be obtained free from other dehydrogenases.

Obviously only experimental investigations can solve the question whether one or several enzymes are responsible for the other dehydrogenations which have been observed besides that of the succinic acid. One reason in favor of several enzymes is the decided specificity typical of the succino-dehydrogenase. The conclusions which might possibly be drawn from this fact, point to other enzymes in the enzyme mass being of a fairly well-pronounced specificity.

But this must not be regarded as indicating absolute specificity. Already in the case of succino-dehydrogenase I have found that not only the succinic acid can be activated. Under the influence of the succino-

dehydrogenase even methylsuccinic acid will show some power of decolorizing methylene blue.

Consequently it is not impossible that the dehydrogenases form a group of enzymes of which each individual influences its own metabolite, or perhaps a small group of such substances, or possibly, of other related substances.

With help of the Mb.-technique described above other tissues than muscle were also investigated in my laboratory. The result was that all tissues contain dehydrogenases. Here only the results in some special cases may be mentioned.

5. THE DEHYDROGENASES OF THE WHITE NERVE SUBSTANCE

It is a well-known fact that science has long hesitated to ascribe to the white nerve-substance an oxygen consumption. But in 1903 certain German investigators: Garten, v. Baeyer and Fröhlich, gave indirect proofs that such consumption must be assumed. In 1904 I was able to give direct proofs with the help of my micro-respirometer that such consumption of oxygen is going on and even to ascertain, at least approximately, the quantity consumed. Some years later, in 1923, I tried to find out whether the mechanism of this oxygen consumption is the same as in the case of other tissues. Using my Mb. method I showed that the usual dehydrogenases are present in the white nerve-substance also. The dehydrogenases of the nerve are thus able to activate succinic acid, glycerolphosphoric acid, lactic acid, citric acid, glutamic acid, and α -ketoglutaric acid. Contrary to what happens in the case of muscle substance, glycerolphosphoric acid is more strongly activated by the white nerve-substance than succinic acid is.

The fact that citric acid is activated by the white nerve-substance is doubly interesting considering that citric acid is

present in the cerebrospinal fluid, as will be shown below.

6. THE LENS SYSTEM

Dehydrogenases are also to be found in the lens, an organ, which as we now know, shows a small but certain oxidative metabolism.

Dehydrogenases effecting the oxidation of fumaric, malic, glycerophosphoric, lactic, citric and acetic acids and the amino acids alanine and valine have been found by Ahlgren to exist in the lens.

The lens was, however, lacking in succino-dehydrogenase, which enzyme has been observed in all other tissues tested. This would seem to indicate that the metabolism in the lens to a certain extent follows a different path from that of muscles and other tissues. The lens-cortex showed a greater oxidation intensity than the lens-nucleus.

From my investigation of the dehydrogenases I concluded that *these enzymes are chemical tools of universal importance in the life of every cell*. This leads to the question to what extent this discovery must change our conception of the metabolic processes in the cells and, more particularly, of the oxidative destruction of the food stuffs. When trying to find the answer to this question I was driven to contradict the current views of the genetic relation between the free oxygen from the atmosphere and that bound in the carbon oxide formed by the living cells.

7. GENERAL VIEW OF THE FINAL FATE OF THE CONSUMED OXYGEN AND OF THE ORIGIN OF THE OXYGEN IN THE EXPIRED CARBON DIOXIDE

Two questions of interest here are: 1. What is the ultimate fate of the *free* oxygen which we breathe, i.e. which are its final products? and 2. What is the origin of the oxygen forming part of the carbon

dioxide which we give off? According to current physiological views the answers to these queries are as follows. The most important final product of the consumed free oxygen is the carbon dioxide. Only a small part of the oxygen takes the form of water. The proportion between the part of the consumed oxygen found in the expired carbon dioxide and the part which has formed water is reflected in the respiratory quotient.

The term "respiratory quotient" was coined by Pflüger in 1877 and defined by him as the relation between the oxygen in the carbon dioxide and the oxygen consumed at the same time. Soon afterwards Zuntz in his standard work on the respiratory metabolism in Hermann's Handbook wrote as follows. "When by the oxidation of carbon one volume oxygen gives one volume carbonic acid the respiratory quotient shows clearly how much of the oxygen consumed is used in the oxidation of carbon and how much goes to that of other substances, especially hydrogen."

According to my opinion we have to change fundamentally our views on these things. I consider that nothing of the oxygen consumed in the general metabolism is found in the expired carbon dioxide. I consider the catabolism of the food stuffs to take place in a series of continuous dehydrogenations, carried out by a series of dehydrogenases. This procedure, to which the complicated food-stuff molecules are thus subjected, might be compared to what happens in modern factories where a piece of metal glides along on rails from workman to workman each of whom has his special task to carry out in the course of the work until the metal piece leaves their hands as a finished product.

When oxygen is present the hydrogen split off by the dehydrogenases is transported to this oxygen with formation of water.

This oxidative catabolism of the food stuffs is characterised not only by this series of dehydrogenations but also by two other processes, viz. addition of water and the splitting off of carbon dioxide. Through the addition of water the intermediate product of the catabolism receives two atoms hydrogen and one atom oxygen. When the water has been added a new dehydrogenation process takes place and two atoms hydrogen are split off once more. Thus the result is a product which in comparison with the original substance is richer in carbon and poorer in hydrogen and which also shows a change in the proportions between carbon and oxygen in favor of the latter element. Through the splitting off of the carbon dioxide the chain of carbon atoms is shortened step by step.

According to this view of the intermediate metabolism, the food stuffs take part in it on account of their actual or potential content of hydrogen. The carbon of this carbon chain has the same function with regard to the hydrogen as the string for the pearls on it. Although the carbon is never directly oxidised in the metabolism its caloric content and its energy is made available through water addition and the splitting off of hydrogen and its oxidation. For the total fund of energy it is of no importance in what way the oxidation is carried out.

I shall now return to the question referred to above concerning the final products of the oxygen and the origin of the oxygen found in the expired carbonic acid.

With regard to the fate of the oxygen the answer to this question is that the oxygen is used for the oxidation of the hydrogen which is activated by the dehydrogenases and given over to the oxygen in activated form. *The oxygen consumed during the respiration is transformed to water.*

Hydroperoxide must be the first, or at least the most important product of this reaction between hydrogen and oxygen. It is the most natural combination product of hydrogen and oxygen in the form available here. However, the formation of hydroperoxide means that the oxygen is half used. This being so, the function of the catalase is easily understood. Through the action of this hydrogen-peroxide-splitting enzyme half of the oxygen of the hydrogen peroxide is liberated and can thus function as hydrogen acceptor once more. Thus the catalase is an enzyme which renders possible a more economical use of the oxygen. This theory—which does not exclude other explanations—harmonizes with the small content of catalase in such organisms as are adapted to life without oxygen.

The oxygen in the expired carbon dioxide does not originate from the oxygen in the atmosphere but comes from other sources.

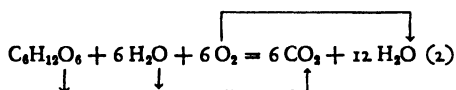
Part of it comes from the oxygen which is originally a content of the molecules of the food stuffs and which remains in its combination with the carbon atoms of the carbonic chain, when the hydrogen atoms are split off by the dehydrogenases. Another part of the oxygen in the expired carbon dioxide is due to the water molecules added to the carbonic chain, particularly in those places where double bonds are formed by dehydrogenations as well as by the change of the aldehyde groups to aldehyde hydrates. It is, of course, quite possible that the water thus added comes from the water formed by the reaction between the oxygen of the atmosphere and the hydrogen of the food stuffs. But the water formed in this way is so small a fraction of the total water content of the organism that it is of no account.

In this connexion I should like to say a

few words about the usual reaction formula for the oxidation of a carbohydrate, e.g. glucose.



Naturally this formula is correct if it claims to show only the new products found in a reaction mixture where glucose is burned and to show the stoichiometric relations between the substances in the formula. But if we want the reaction formula to give the *genetic* relation between the atoms on both sides of the equality mark in the equation, then the equation is unsatisfactory. It does not express the biological oxidation of the glucose, such as I have interpreted it. The formula must then be amplified and water must be introduced in the following way.



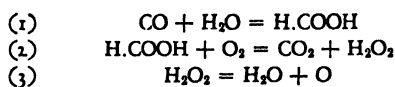
The formula (1) can be criticised from the genetical point of view on the ground that six of the twelve atoms of oxygen which are denoted as forming part of the carbonic acid on the right side of the sign of equality do not come from the glucose but from a substance—water—which is not denoted in the formula. Consequently the formula is not to be looked upon as the result of an abbreviation due to the leaving-out of intermediate links—which, of course, is allowed—but is incorrect, in that it suggests a genetic relation which does not exist.

Formula 2 is faultless from this point of view but without further amplification it is of no great value. On this ground I have tried to explain it by putting in lines of connexion and arrows in order to make clear the genetic relations between the atom groups which are of interest here.

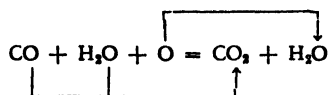
This opinion of mine that oxygen con-

sumed by a certain oxidation process is changed to water and that the oxygen in the carbon dioxide comes from the oxidized substance or from the added water, is perhaps somewhat surprising. It is however supported by certain well-known processes from organic chemistry.

As early as 1886 Dixon showed that water probably participates in the usual oxidation process of carbon monoxide. In its dry form carbon monoxide reacts with oxygen only at very high temperatures. For the oxidation of carbon monoxide at the temperature of an ordinary flame the presence of water is absolutely necessary. The reaction which takes place under these conditions shows the following stages, as has been shown later by Wartenberg and Sieg.



Leaving out irrelevant links and using the same method as previously for denoting genetical relations between the atom groups of interest here, we must, in my opinion, arrive at the following results:



Thus the free oxygen of the atmosphere gives here also water as its final product. The oxygen in the carbon dioxide comes from the oxygen partly in the carbon monoxide, partly in the water.

With regard to this general conception of the final fate of the oxygen consumed it may be objected that it has not yet been proved. This is true but the objection applies even more to the older view. In support of the conception which I have outlined above it may be pointed out that, as far as experiments in this field are available, they harmonize well with my theory.

Thanks to the work of the Cambridge school we now have at our disposal methods for extracting it from the milk in a concentrated form and—as far as we are able to judge—free from other dehydrogenases, with the exception perhaps of the Schardinger enzyme.

The biological substrates of this enzyme are xanthin and hypoxanthin. These substances seem to exist, at least to a certain extent, in their hydrate forms. The xanthin dehydrogenase transforms them to uric acid by depriving them of certain hydrogen atoms. The investigations of this enzyme have further shown that the action of this dehydrogenase also is characterized by pronounced specificity. It seems to have a weak oxidising power on adenin and, among the substituted purines, on 6-8-dihydroxipurine and 2-thioxanthine, besides its normal effect on hypoxanthine and xanthine. If a methyl group is introduced into the pyrimidine or iminazole ring this is sufficient to prevent activation entirely.

Perhaps there exists one exception to this high degree of specificity. The enzyme preparates obtained hitherto are able also to activate aldehydes, and thus give the typical Schardinger reaction. It may be possible, though, that the xanthin dehydrogenase and the aldehyde dehydrogenase are different enzymes, but with physical characteristics so nearly identical that the two substances can be isolated only with difficulty.

In 1924 Dickson and Thurlow showed that certain purines, in spite of not being activated by the dehydrogenase, are absorbed on its surface. In this way they prevent the dehydrogenase from activating the hydrogen of xanthine and hypoxanthine. This makes a separate study possible on one hand of the absorption of certain substances on the enzyme and, on the other, of the activation of the substrate by

the enzyme. If the Mb. is reduced, the purine substance must have been activated; if, on the other hand, the velocity of the reduction generally obtained by means of the xanthine is decreased when another purine substance is added, then an absorption of this other substance upon the enzyme must have taken place.

As pointed out by Sir F. G. Hopkins, the oxidation of xanthine and hypoxanthine to uric acid is a reaction which is difficult to obtain by the usual oxidising reagents. As a matter of fact, no one seems to have been able to do so. The explanation of this peculiar oxidation effect seems to be the same in the case of the xanthine substances as in that of succinic acid—viz. the activation of hydrogen.

9. THE DEHYDROGENASES OF BACTERIA

As pointed out in the introduction to this lecture the oxidation of alcohol to acetic acid by the acetic bacteria was one of the biological reactions on which Wieland founded his theory of biological dehydrogenation. But since then our knowledge of the bacteriological dehydrogenation processes has made great progress. This is due to the work of J. H. Quastel and his collaborators, Stephenson, Whetham, Woolf and Wooldridge, working in Sir F. G. Hopkins' Institute in Cambridge.

Quastel used the bacteria under such conditions that their growth during the experimental period was small or non-existent. In other words he used "non-proliferating" bacteria. With help of such bacteria he was able to study the simple katabolic processes without complication of the anabolic processes resulting in the formation of new cell substance. What he studied, using the non-proliferating bacteria, was then comparable to the metabolic processes in tissues from full grown higher organisms. Quastel calls the non-proliferating bacteria also "rest-

ing bacteria," regarding them as comparable with resting muscles and other tissues. I myself prefer not to use the name "resting" bacteria. The non-proliferating bacteria are, with regard to their metabolism, comparable with non-growing tissues, resting or non-resting, independent of their degree of activity.

The conditions, that growth shall be small or absent during the experimental time, are easily secured, if the experiments are carried out:

1. In the absence of some factor essential for growth, e.g. a nutritive source of nitrogen in the culture.

2. Anaerobically.

3. In a short time—usually under thirty minutes.

4. At a relatively high temperature (i.e. a temperature at which growth is known either to be inhibited or not to occur, but which does not seriously interfere with the reaction under investigation.)

Bacteria used under these conditions lend themselves to investigation in the same manner as enzymes or other catalytic systems, and it has been possible to show that the bacteria suspensions have many factors in common with enzyme systems. The easy manipulation of non-proliferating bacteria, and the fact that conditions can be well controlled, make it possible to obtain reproducible and consistent results.

Among the results arrived at by Quastel and his collaborators during the course of their experiments on *Bacillus coli* may here first be mentioned their discovery of a great number of organic substances activated by *B. coli*. Using the Mb. technique Quastel found that 56 substances could be activated, although these substances otherwise are quite inert, apart from the influence of living cells.

When drawing his conclusions from these observations Quastel makes a mis-

take, which, however, is a fortunate one. His mistake is that he credits me with the opinion that every activated substance requires each its absolutely specific enzyme. According to him my opinion would be that these 56 activated substances should require 56 specific enzymes.

Quastel is quite right in regarding this as highly improbable. Among the substances activated by *B. coli* are several which cannot be supposed to exist in the usual media. That the bacillus should have at its disposal specific enzymes for these substances can be excluded. As is evident from what has been said above, I have on the contrary distinctly repudiated the idea of absolutely specific enzymes. It is true that I hold a pluralistic view of this class of enzymes, but this does not mean that I believe in absolutely specific enzymes. Quastel's mistake, which he shares with other authors, is probably due to some unsatisfactory abstract of my original, difficultly accessible paper.

I said just now that Quastel's mistake was a fortunate one. It has led him to an interesting explanation—useful at least as a working hypothesis—of the mechanism by means of which the bacteria activate the hydrogen of the various substances.

According to him the dehydrogenations are primarily due to polarisations of substrate molecules induced by electrical fields which characterize particular centres—the "active centra"—of cellular and intracellular surfaces. If the polarisation is effective enough, the molecule may in that way become a hydrogen donator or acceptor.

In order to understand Quastel's conception of the active centra of the cells, it is perhaps best to start from an opposite and simple chemical view of the dehydrogenating enzymes. Let us thus consider them as protein molecules with a certain

group, specific for the enzyme character. We can call it the "prosthetic" group.

For Quastel the dehydrogenetic actions of the cells do not generally depend on such a simple molecule but on the existence of a certain structure, in other words on a complex of molecules forming a relatively stable physical aggregate. As is the case in many solid mechanical systems the structure of a living cell and especially of its surface also may be the seat of a certain strain between the constituting molecules. A local production of an external electric field then will take place with a polarisation effect on such substances, which through their constitution have access to the field. These substances are in other words activated.

This view of Quastel has formed a working hypothesis for a great number of investigations which have considerably widened our field of knowledge concerning the factors influencing the hydrogen activating powers of the bacteria.

An interesting result of these investigations was the establishing of the fact that the destructive action of different factors is highly selective. Under influence of a certain factor *B. coli* may lose its dehydrogenating power with regard to a certain substance without changing it regarding another. A step by step degradation occurs. Bacteria treated with ether or toluol lose their power to activate sugar, acetic, gluconic and glutamic acids, but keep unchanged their power to activate formic, lactic and succinic acid.

It seems very probable, that Quastel's ideas regarding the "active centre" are due to his working with bacteria. In these small organisms the surface is of comparatively more account than in bigger cells. The bacteria are scarcely anything more than a surface-membrane. The first and quite necessary function of a cell membrane is to prevent the dissolution of the

cell in its fluid medium. Hence their stable structure.

In the case of such cells it is tempting to look upon the solid structure as essential for functions which in other cells are not necessarily bound to a structure.

If we work on larger cells and on tissues of softer consistency we are not so easily tempted to attach such a high importance to the cell structure for the dehydrogenation processes. No great change is found in the dehydrogenation processes if we place the cells in hypotonic fluids. The water which is then taken up must penetrate between the colloidal molecules and effectively change the existing intermolecular strain. Were this strain of great importance, the dehydrogenation would be much altered. From such cells it is also more easy to extract the dehydrogenases in soluble form. Here they show their power to work independent of a structure.

To go back to the step by step narrowing of the action field of the dehydrogenases under the influence of some destructive factor, it seems not to exclude even the simple assumption that the dehydrogenase influenced is a simple protein molecule with an active prosthetic group. As the various haemoglobins have different qualities and as the oxygen combining peculiarities of a certain haemoglobin can be changed by influencing its protein group, so the difference, due to factors influencing the protein component of the dehydrogenase-molecule, may be able to change the field of action of the enzyme.

10. THE DEHYDROGENASES IN SEEDS

A great number of seeds contain stores of dehydrogenases. In certain seeds they occur in such form that these seeds are the best material for the detection of dehydrogenases and for the study of their qualities.

If the resources of the Mb. technique

are available it is sufficient, in order to show certain dehydrogenation reactions, to place the necessary amount of Mb.-donator-solution and of pulverized seed in a vacuum tube. After the evacuation of the tube and the placing of it in a thermostat the decoloration characteristic of the dehydrogenases will soon occur. In many cases it is better to use a water solution or a salt solution of the seed instead of the pulverized seed. A neutral potassium phosphate solution is often particularly suitable.

Different seeds behave very differently during these experiments. Thus, seeds show great differences in the velocity of their "spontaneous decoloration," i.e. the decoloration of the reaction mixture under the conditions of the Mb. technique but without the addition of a special donator. This spontaneous decoloration as a rule is, e.g., considerably greater in the case of peas than of cucumber seed.

Naturally these enzymatic decoloration processes must be distinguished from others of non-enzymatic origin—not requiring dehydrogenases and hydrogen donators. Thus in my experiments with seeds from *Acacia lophanta* I found a particularly strong Mb. reduction, which however did *not* show the sensitiveness to temperatures above 60°C. characteristic of the dehydrogenases. When the pulverized seed was mixed with a phosphate solution a strong smell of onions appeared. It is tempting to connect the strong reduction effect with the presence of some reactive volatile substance.

When such substances which may possibly act as donators are added to the mixture in the tubes, the decoloration process varies in different seeds.

In many cases there is no effect on the Mb. even when a great many substances are tested. Obviously continued testing

might lead to the discovery of some donator. It is possible also that with some other acceptor than Mb. one or the other of the tested substances would reveal itself as a donator. Very often the existing spontaneous decoloration and the lack of effect when some donator is specially added, may be due to the fact that the system already possesses donators in optimal amount. In such cases the addition of more donators has naturally no effect. Some kinds of seeds are, however, very sensitive to an addition of suitable donators.

Seeds which are at all sensitive to donators behave differently towards different donators. Experience has shown that certain substances will act as donators more often than others. Thus formic acid, malic acid, glutamic acid, hexosediphosphoric acid, and ethyl alcohol are active on a number of seeds, but the degree of their activating power varies. Malic acid may be more active than, e.g., alcohol in one case, but in the case of another seed the conditions may be reversed.

It is a rather remarkable fact that I have found no trace of activating power on seeds in the case of succinic acid, which is such a strong activator where animal tissues are concerned. Once I thought I observed such an effect in the case of succinic acid, but it turned out to be due to the effect of malic acid present in the succinic acid preparation.

As a rule the seeds used have been very slightly sensitive to simple or compound carbohydrates. But they are all the more sensitive to the addition of hexosediphosphoric acid—but not to hexosemonophosphoric acid. Perhaps the strong effect of the hexosediphosphoric acid is due to the change of the carbohydrate molecule into a polyvalent ion. Probably the high electric charge of such an ion brings about

quite different conditions of adsorption than those existing in the case of the neutral molecule.

A point which must always be considered during these researches is the following: Is the substance with apparent donator effect a real donator, or does it obtain this power only after some change or other?

The results mentioned above are most easily interpreted from a pluralistic view of the dehydrogenases. Probably seeds possess a series of dehydrogenases, each with a limited field of action. Different seeds may possess the same or different dehydrogenases.

The question of the degree of specificity of each enzyme may be left open. I consider it possible that enzymes may possess different degrees of specificity in different seeds. I have found, e.g., some seeds which are strongly activated by ethyl alcohol but not at all by propyl alcohol. Other kinds of seeds are activated by ethyl alcohol as well as by propyl alcohol, though the effect is less strong in the case of the latter substance.

It is possible that in the case of this seed there are two enzymes, one for ethyl alcohol and one for the propyl alcohol. Perhaps the enzyme in the latter case is less specific.

The hypothesis that different seeds possess different specific enzymes is supported by the fact that some seeds are activated by substances which lack every trace of activating power in the case of most seeds.

Citric acid, e.g., behaves as a particularly effective activator in the case of cucumber seeds, while I have observed no effect of this acid on the other seeds, which I have investigated (with the exception perhaps of *Malva* seed). Oxalic acid shows a clear if not a specially strong activating power in the case of seeds of some species of *Malva* and, perhaps, of two other plants

also. But as a rule citric acid as well as oxalic acid are not only incapable of hastening the enzymatic decoloration process of seed extracts, they even retard it in many cases.

Similar effects of inhibition are not unusual when substances chemically rather inactive are added. The inhibition is probably caused by the adsorption of these substances on the surfaces of the dehydrogenases, although these substances are not activated. By this adsorption the inhibiting substances cause the real donators to be removed from the activating surfaces.

Thus we discover in the case of the dehydrogenases of seeds the same effects which have been studied with such great success by Dixon and Thurlow in the cases of the xanthine dehydrogenase and by Quastel and collaborators in the case of bacteria.

II. THE DEHYDROGENASES OF POLLEN

In order to understand the function of the dehydrogenases it is necessary to investigate as many types of cells as possible; above all, no cell type with a distinctly specific function must be left out of consideration.

I have therefore included in my investigation also the sex cells. Up till now I have only had time to investigate the pollen of hazel (*Corylus avellana*). It was easy to show the existence of dehydrogenases in these cells. The dehydrogenases found were able to activate malic acid, glycerophosphoric acid, and certain alcohols, especially ethyl alcohol, propyl alcohol and normal butyl alcohol.

12. SOME FURTHER REMARKS ABOUT THE SPECIFICITY OF THE DEHYDROGENASES

When in my earliest papers I expressed a pluralistic view of the nature of the dehydrogenases, I based my opinion on the observation that it was possible to obtain

a succino-dehydrogenase preparation with powerful action on succinic acid but without power to activate the great number of other metabolites investigated by me. Further investigation has revealed the fact that the dehydrogenase preparation which I used is able to activate also glycerin-phosphoric acid and hexosediphosphoric acid. But this does not necessarily point to the assumption that these substances are activated by the succino-dehydrogenase itself. The simplest and most likely explanation is that the succino-dehydrogenase preparation contains also one or more other dehydrogenases. I leave it an open question whether the glycerin-phosphoric acid and the hexosediphosphoric acid are activated by the same dehydrogenase or by different ones. The fact that the succino-dehydrogenase does not influence these substances is evident, since it is possible to obtain from seeds preparations which have a very strong activating influence on hexosediphosphoric acid and a noticeable influence on glycerin-phosphoric acid but none whatever on succinic acid.

It has been objected that the dehydrogenase preparations made according to the method which has been described by Andersson from my laboratory, do not show the specificity which, according to what has been said above, ought to characterize the succino-dehydrogenase. They will activate also, e.g. lactic acid. However the preparation according to the method described by Andersson is not intended to show the highest degree of specificity. The aim of this method is only to obtain in an easy way a succino-dehydrogenase preparation which will show the characteristic effect of this enzyme on succinic acid. If a preparation of the highest possible specificity is required, the material used must be subjected to a much more effective washing.

A good evidence for the specificity of the succino-dehydrogenase is, also the fact that the lens substance of the eye activates lactic acid, malic acid, citric acid, and glycerin-phosphoric acid, but has no power to activate succinic acid, as shown by Ahlgren.

The investigations from the laboratory of Sir F. G. Hopkins also point to a high specificity of the xanthin-dehydrogenase. And this same laboratory has lately furnished further proofs for the truth of the theory of the high specificity of the dehydrogenases. Thus Miss Marjory Stephenson has succeeded in obtaining from *Bacillus coli* a specific soluble lactico-dehydrogenase. *Bacillus coli* was cultivated on a suitable substrate containing sodium lactate and, after being thoroughly washed, was left to autolyse for a number of days in a phosphate solution and then centrifuged. The clear supernatant liquid was found to contain a lactico-dehydrogenase with a small power to activate also α -hydroxybutyrate. Further, Bernheim has been able to extract a soluble citrico-dehydrogenase free from other tissue-dehydrogenases. He used fresh liver substance from oxen, sheep and pigs, which substance, after being minced, was dehydrated by acetone, and when the dry liver powder was extracted with water this solution contained only citrico-dehydrogenase but no other dehydrogenase. But if the solution is made with di-sodium phosphate, both xanthine-dehydrogenase and succino-dehydrogenase are found in the solution.

Bernheim has also been able to obtain a lactico-dehydrogenase in soluble form and free from other dehydrogenases by extracting acetone-dry yeast with phosphate solution for a short period. If the extraction is carried on too long, the succino-dehydrogenase also is extracted. The lactico-dehydrogenase obtained has also a certain power to activate α -oxybutyric acid.

13. THE BEHAVIOR TOWARDS OXYGEN OF THE
HYDROGEN ACTIVATED BY THE
DEHYDROGENASES

The salient point of the oxidation theory of Wieland is, in my opinion, the view that the oxidation of the dysoxidisable substances is made possible by the activation of their hydrogen. Wieland finds no reason to assume also an activation of oxygen for the oxidation processes he has studied. In his opinion the hydrogen activated by the catalyser can react with the unchanged inactive oxygen. For the oxidation processes investigated by me I have on the whole accepted Wieland's theory. However, during my earliest experiments I made an observation, which was difficult to explain without assuming a certain activation of the oxygen also. As is known from the investigations of Battelli and Stern, KCN inhibits very effectively the enzymatic oxidation of succinic acid in an O_2 -medium. Investigating the effect of KCN on the oxidation of succinic acid in vacuo in the presence of Mb., I found that this process was not inhibited by KCN. This last very peculiar fact led me to conclude that KCN does not affect the succino-dehydrogenase. In order to explain the inhibitive effect of KCN, which in spite of the insensitivity of the dehydrogenase for KCN was observed in the first case, I formed a hypothesis based on the assumption that a certain activation of oxygen is also necessary for this reaction between hydrogen and oxygen. On the basis of the views of the kinetic gas theory I felt entitled to conclude that of the oxygen present in the reaction-mixture a small part occurs in an activated form due to the collision of the molecules. It is this "spontaneously activated" part of the oxygen which, in my opinion, was able to serve as acceptor for the activated hydrogen in my experiments. On the other hand, this small part, to the extent

it does occur, is being continuously inactivated, when KCN is present.

The facts under discussion here have also been explained in other ways. In 1928 Wieland and Bertho launched the explanation that through its adsorption on the dehydrogenases Mb. has the power to expel the KCN from these enzymes and thus prevent its effect.

The question whether hydrogen activated by the dehydrogenases is accepted by unactivated oxygen has been further illustrated by certain new observations.

Certain dehydrogenase solutions do not react with the oxygen of the atmosphere, although they react with Mb. But this distinction does not exist in the case of the dehydrogenases still bound to the cells. Miss Marjory Stephenson has thus found that the lactic acid dehydrogenase still bound to the bacteria can transport the hydrogen to the oxygen of the atmosphere. If, on the other hand, this dehydrogenase is brought into solution, it loses this power but is still able to reduce Mb. Bernheim has reached a similar result in the case of the dehydrogenase of liver substance and of the lactico-dehydrogenase from the tissues of the higher animals.

In the case of the succino-dehydrogenase and the xanthino-dehydrogenase the observations of different investigators contradict each other. In the laboratory at Lund we have worked with succino-dehydrogenase solutions which were still able to use the oxygen of the atmosphere. Von Euler has published the observation that succino-dehydrogenase solutions often lack this power, while not only some but all of the solutions prepared by Miss Stern are recorded to be ineffective in this respect. Regarded in connection with the generally accepted fact that, so long as they are bound to the cell substance, the dehydrogenases have in every case the

power to use the oxygen of the atmosphere, the observations of Stephenson, Bernheim and others point to the presence in the cells and tissues of an insoluble factor or of a factor which is dissolved only with difficulty or as an emulsion, a factor which must be responsible for the reaction between the activated hydrogen and the oxygen.

On this point the excellent investigations of Keilin have a great significance. Keilin has found that cells of aerobic organisms contain a respiratory pigment, cytochrome, and also a real oxidase, which he calls the indophenol oxidase. These two substances collaborate in the following way. The indophenol oxidase is able to transfer oxygen to the cytochrome and thus to change it to its oxidized form. It is this oxidized cytochrome which in its turn has the power of reacting with the hydrogen activated by the dehydrogenases. The cytochrome-indophenol-oxidase system seems difficult to extract and bring in the form of a solution. In the still intact cells and tissues the dehydrogenases collaborate with this system and are thus able to use the oxygen of the atmosphere. Solutions of dehydrogenases, on the other hand, lack the cytochrome system and are scarcely able to use the oxygen.

Keilin has shown that the indophenol oxidase is rendered inactive by KCN, while this substance does not affect the dehydrogenases. Thus the difference between the action of KCN on the O-oxidation and on the Mb.-oxidation is explained in a very interesting way.

14. FURTHER FUNCTIONS OF THE DEHYDROGENASES

In describing the dehydrogenases Wieland realized that a series of different effects must be ascribed to this new group of enzymes. In transporting hydrogen from the donor substance to the accep-

tor substance the dehydrogenase acts both as an oxidase and a reductase. This means that the assumption of the existence of special reductases must be given up. Wieland pointed out that these enzymes can also transfer hydrogen from one molecule to another of the same substance. Thus two molecules of an aldehyde can be brought to react with one another in such a way that the one molecule is changed to the corresponding alcohol and the other to the corresponding acid. In this way is brought about what is termed a mutase effect or a "disproportionation" (in German "*Disproportionierung*"). That is to say, what have hitherto been called "mutases" are in reality dehydrogenases. The biological Cannizzaro-reactions hitherto observed may be said to be due to dehydrogenases.

When I first began my investigations in this field I suggested that this enzyme group may also be able to carry out syntheses of short carbon chains to longer ones. Having observed the enzymatic dehydrogenation of acetic acid and having found it difficult to explain in any other way, I formed the hypothesis that two molecules of acetic acid giving off two hydrogen atoms are linked together to form one molecule of succinic acid. This hypothesis has played a part in the discussion of the routes of the intermediate metabolism, and given rise to special investigations. It has been possible to bring about this synthesis in model experiments in vitro without the help of enzymes and certain bacteria are also able to perform it. But up to now its presence in the tissues of the higher organisms has not been proved. This may possibly be due to a difficulty in finding the suitable hydrogen acceptor and in preventing the simultaneous transformation of the succinic acid eventually formed.

This enzyme group is of special interest

also on account of the reversible processes to which it gives rise.

When succinic acid is being transformed to fumaric acid under the influence of the succino-dehydrogenase, there takes place at the same time and under the influence of the same enzyme a transformation of fumaric acid to succinic acid. The quantitative relation between the two contrary processes depends on the relative amounts of the two substances.

That is to say: the succino-dehydrogenase is at the same time a fumarico-hydrogenase. Such considerations as this seem to excuse the name "hydrogeno-transportase" which I have allowed myself to give to this enzyme group.

The first to investigate the reversible processes just referred to were Quastel, Stephenson and Whetham. They used *B. coli*. Later I myself, using the succino-dehydrogenase of muscle substance, studied the equilibrium between succinic acid and fumaric acid.

The oxidation-reduction processes or, if you do not object to this short form, the redox processes carried out by the dehydrogenases may be measured by electrical methods.

For the history of the electric potentials due to the redox processes of living cells or of biological enzyme systems I refer my audience to the excellent works of Clark, Needham and Needham, and Michaelis.

15. THE USE OF THE Mb. TECHNIQUE IN QUALITATIVE AND QUANTITATIVE ANALYSIS

It is clear from what has been said above that the reduction of Mb. in vacuo requires the presence of a donator substance as well as of the corresponding specific enzyme. The Mb. reduction does not take place when one or the other of these factors is lacking. Mb. + succinic acid give no reduction, nor Mb. + succino-dehydro-

genase. If, on the other hand, the system is made complete so that all the three substances: Mb., succino-dehydrogenase, and succinic acid, are present, then the reduction is certain.

This fact enables us to use the enzymatic decoloration in question in the service of biochemical analysis. If we add a substance of unknown composition to a solution of Mb. and succino-dehydrogenase and no decoloration follows, it is a fairly safe conclusion that the unknown substance contains no succinic acid. But, when the result is a decoloration there is reason to suppose that the unknown substance contains succinic acid.

The question to what extent the reduction caused by an unknown substance in the system Mb. + dehydrogenase makes the presence of succinic acid probable or certain, is intimately bound up with another: viz. that of the specificity of the succino-dehydrogenase solution employed.

Were it possible to use a pure succino-dehydrogenase free from all other dehydrogenases and if the succino-dehydrogenase could be considered as being absolutely specific, then the appearance of an enzymatic decoloration when an unknown substance is added would be a certain evidence for a content of succinic acid in the substance employed.

However, neither of these two assumptions is fully realized. At present it is impossible to obtain a chemically pure solution of succino-dehydrogenase. But this is of minor account. A more important fact is that all succino-dehydrogenase solutions have been found to contain other dehydrogenases also. In addition they contain an enzyme active on glycerolphosphoric acid. Lately it has been found that the succino-dehydrogenase solution made from muscle substance in the usual way is able to activate also hexose-diphosphoric acid.

Even if we should succeed in obtaining a succino-dehydrogenase solution free from other dehydrogenases, we should not be entitled to attribute to it an absolute specificity. Besides succinic acid the dehydrogenase seems to activate also methyl-succinic acid.

But although these circumstances influence the certainty of this analytic method, they do not invalidate it altogether. But they make certain precautions necessary. If, then, an unknown substance added to a solution of Mb. and succino-dehydrogenase will cause decoloration, special experiments are necessary in order to show whether the decoloration is due to succinic acid, to glycerin-phosphoric acid, or to hexose-diphosphoric acid. The fact that in order to cause a decoloration the glycerin-phosphoric acid must be much more concentrated than succinic acid, enables us often to exclude the possibility of glycerin-phosphoric acid. If, then, a very small amount of a substance will cause decoloration, it is very improbable that the glycerin-phosphoric acid is the responsible factor.

In order to find out whether a decoloration process is due to the succinic acid or to the hexose-diphosphoric acid, it is possible to use another dehydrogenase system. From certain seeds we are able to obtain dehydrogenases activating hexose-diphosphoric acid which have no influence on succinic acid. If an unknown substance causes reduction of the Mb. succino-dehydrogenase system obtained from muscle substance but has no effect on the dehydrogenase system from seeds it must contain succinic acid and cannot contain hexose-diphosphoric acid.

In 1917, before we knew that the succinic dehydrogenase preparations contain also dehydrogenases activating glycerin-phosphoric acid and hexose-diphosphoric acid, I made some experiments with the

method just described in order to detect a possible content of succinic acid in animal tissues and fluids.

A great advantage with this method is its sensitiveness. Factors in this sensitiveness are (1) the relation between the molecular weights of succinic acid and Mb., respectively, and (2) the lowest concentration, in which Mb. can still give a solution showing appreciable color.

The value of the molecular weight of the succinic acid can be put at 118.1 and the same value for Mb. at 336.4. Since one molecule of succinic acid is sufficient to change one molecule Mb. to its leuco-form, one part succinic acid is sufficient to decolorize three parts Mb.

Regarding the question, what is the least amount of Mb. still detectable in water, it may be said that it is still possible to detect the blue color of one cc. of Mb. solution at a dilution of 1:1000000. One cc. of such solution contains only 0.001 mgm. Mb.,—i.e. one microgram (= 1 γ). This amount of Mb. requires for decoloration only 0.33 microgram of succinic acid. Theoretically it would be possible to detect even this small amount of succinic acid with the help of the Mb.-dehydrogenase method. In my practical work I found it advisable to limit the sensitiveness of the method to 20 micrograms of succinic acid.

During experiments with this method I met some difficulties when trying to extract the small amounts of succinic acid present in the tissues. The experiments were for this cause postponed. But during the ten years which have elapsed since these experiments were first begun I have never given up the idea of using the Mb.-dehydrogenase systems for analytical work and about a year ago I succeeded in finding a Mb.-dehydrogenase system which seems to make possible the determination of citric acid in animal tissues

and fluids in very small amounts not detectable with other technical methods.

The technique is based on the presence in cucumber seeds of a dehydrogenase with the power to activate citric acid. When a perfectly fresh phosphate solution of cucumber seeds of a convenient sort, to which Mb. has been added, is investigated by means of the Mb. technique, its spontaneous decoloration will be found to be very small. The fact that the decoloration is small is not due to the absence of active enzymes but obviously to the small quantity of donator substances. This is proved by the fact that the velocity of the decoloration process is considerably increased when certain hydrogen donators are added. The dehydrogenases in the cucumber seed extract were obviously in need of donators. The most important donators for this extract are malic acid, ethyl alcohol, glycogen, dextrin, hexosediphosphoric acid, and citric acid. Citric acid and hexosediphosphoric acid form a group by themselves on account of their capacity of serving as donators for the dehydrogenases of the cucumber seeds. Only very small quantities of these substances are necessary in order to reach the maximal velocity of decoloration which is ever obtainable with these substances. As regards the effect of citric acid and malic acid, it is possible to obtain with both these substances the same high decoloration velocity but in order to achieve this result we must use 250 times as much malic acid as citric acid. As has been pointed out in another connection, malic acid, ethyl alcohol and hexosediphosphoric acid are among the most common of all donators for seeds. But with citric acid the case is quite different. Among the great number of seeds investigated in this respect I have found citric acid active as donator only in the case of seeds from cucumber and from *Malva crispa*, but in the latter case the action was weak.

The discovery of this peculiar reaction of cucumber seeds to citric acid made me ask: Is it possible to base on this fact a method for detecting even small amounts of citric acid in animal tissues and fluids?

Somebody may ask: Is there really need for such a method?

I myself do not hesitate to answer in the affirmative. Having detected, in 1909, the great oxidizing power of animal tissues with regard to citric acid, and, in 1918, the citrico-dehydrogenase, I have since considered it highly probable that citric acid is a normal intermediate product in metabolism. I have ventured the guess that it might be possible to detect citric acid in many animal fluids and tissues, if only methods sufficiently sensitive were at our disposal. Now it seemed possible to make use of this peculiar behavior of cucumber seeds with regard to citric acid in order to detect even small amounts of this substance.

It ought to be mentioned that in 1891 Henkel had detected the presence of citric acid in milk. Further experiments of Amberg, McClure, Mayer, and Woods have shown that citric acid is present also in urine and sweat.

However, the methods used by these investigators are far from possessing the sensitiveness and rapidity of the dehydrogenase method. It is this lack of suitable methods which in all probability has caused the noticeable scarcity, up to now, of investigations concerning the citric acid content in animal fluids and tissues.

The careful investigations of the behavior of cucumber seed extract to Mb. in vacuum which have been carried out at the Physiological Institute of Lund, have shown that if very small amounts of a certain solution have already the power of increasing tenfold the decoloration velocity of Mb., it is in reality out of the question to ascribe this action to any other substances but citric acid or hexose-diphos-

phoric acid. In order to decide to which of these two substances the effect in question is due, it is possible to build on the fact that many seeds react strongly to hexose-diphosphoric acid but not at all to citric acid. Seeds from, e.g., *Citrus aurantium dulcis* (orange) and from *Corchorus capsularis* (jute) behave in this way.

By making use of this relation of cucumber seed extract to citric acid it has been possible to create also a quantitative method for the determination of citric acid in animal fluids. A fact of special importance for this method is that we are able to decide accurately the minimal quantity of citric acid required for the maximal velocity of the decoloration process. If we go below this minimal quantity the decoloration velocity decreases very rapidly. The method is the more convenient and easy since it is unnecessary to extract and isolate the citric acid from the animal fluids. The activity of the cucumber seed enzyme is not—or is only in a small degree—affected by the other components of the animal fluids. With regard to the practical use of the method I will confine myself to a few points. Equal amounts of cucumber seed extract are placed in two series of vacuum tubes. Increasing quantities of a citric acid solution of convenient concentration are added to the one series. To the vacuum tubes of the other series are added increasing quantities of the fluid under investigation. Both series are treated in the way typical of the Mb. technique. By means of the first series we find the minimal quantity of citric acid giving the shortest decoloration time. The second series of tubes will show whether it is at all possible to reach the same short decoloration time with the fluid to be investigated and, if so, what quantity is needed. This series will also show whether the decoloration time can be shortened still more, if we add larger doses of the fluid. If this is the case the effect cannot be due

to citric acid only but some other factor must be at work also. We are entitled to assume the existence in the minimal quantity of fluid required for the decoloration an amount of citric acid equal to that required for the same effect when the acid is added to the pure cucumber seed extract. Special experiments ought to be made from time to time with a view to testing whether an extra quantity of citric acid added to the fluid under investigation can be detected with a sufficient degree of accuracy.

A method must be valued according to the results achieved. What new discoveries have then been made by means of the method just described?

I give here a table showing the citric acid content of some animal fluids. All values are expressed in parts per thousand ("per mille").

ANIMAL FLUID	CITRIC ACID CONTENT IN PARTS PER THOUSAND	INVESTIGATOR
Urine.....	0.25-1.8	Östberg
Citric acid is never absent in urine from healthy people. It may go down to zero in nephritis.....		
Women's milk contains no citric acid before two days after delivery. The citric acid content then increases rapidly to 1.5..		Jerlov
Cerebrospinal fluid.....	0.05-0.06	Benni
Fluid from epididymis of rabbit.....	2.5	Scherstén
Fluid from seminal vesicles of rabbit.....	1.5	Scherstén
Fluid from seminal vesicles of pig.....	6	Scherstén
Sperm of man.....	1.8-4.1	Scherstén
Sweat.....	About 0.1	Scherstén
Blood serum of man.....	Less than determinable	Östberg

With methods similar to that here described other metabolites are being investigated.

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BIOLOGICAL PROBLEMS AND OPINIONS

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HAVING just celebrated the centenary of the first successful attempt at manufacturing an organic product in the laboratory, it is fitting that the eye of scientific men should scan the century, take pride in the marvelous progress of the biological sciences, search for the causes of failure and evaluate experimental evidence and philosophical interpretations. It is further fitting that we should know what the contributions of men of all lands have been, lest we fall into the common error of non-scientific men—that of assuming that because a problem, a fellow worker, an emphasis, or a philosophy of life is close at hand, and thus considered important by friends and co-workers, it therefore takes precedence over all the remaining universe.

The history of science during the nineteenth century has been written so well by those who have preceded us that it would be presumptuous on my part to try to improve upon it. Not so much, however, has been written regarding our own generation, or the work of men still with us. Consequently, this paper is to be confined to a statement of what the ablest present-day workers in the biological sciences believe to be important and well worth while.

Yet here again the field has become so vast, the work so varied, and the contributions so numerous that one may well throw up one's hands in dismay, especially when it is noted that the editors of *Biological Abstracts* have listed forty-seven

major subjects under which to classify the work of biologists. And each of these forty-seven major subjects has at least one or more subheadings or branches of biology in which men are specializing.

If Johannes Müller, as it is often stated, broke down mentally trying to keep abreast of the literature on physiology about the year 1857, when physiology had but just come into existence during his lifetime, how can any one person even approach success in such a plan now, when thousands upon thousands of papers are being published annually?

I do not believe that anyone can do so successfully, nor does this paper make any claims towards furnishing even an approximately complete answer. I have, therefore, asked the heads of departments of biology and zoology in all the universities of the world, outside the United States, and also twenty of our own most distinguished biologists, to give me their mature thought on the matter. This paper, then, represents, not the opinion of any one man, but the consensus of opinion of the world's most important biologists and zoologists.

These same distinguished scientists, leaders in their respective branches of biology from every country of the world, here then speak for themselves. I shall not evaluate, but attempt to state the case and so produce a living document at least of interest to the younger workers in the field.

Seventeen years ago, C. S. Minot of Harvard, then Exchange Professor at the

Universities of Berlin and Jena, delivered six lectures on *Modern Problems of Biology* at the latter institution. The six problems discussed were:

1. The New Cell Doctrine
2. Cytomorphosis
3. The Doctrine of Immortality
4. The Development of Death
5. The Determination of Sex
6. The Notion of Life

A *Survey of National Trends in Biology*, dealing with the problems of biology as they appear to the biologists of all nations seventeen years later, should prove interesting.

It is undoubtedly true that science should know no political boundaries, and that as biology is a science, it should be international. However, one need be in correspondence with but a very few biologists to find that while biology may be international, biologists certainly are not.

In the answers received from the various biologists and zoologists to my query there is reflected the same national feeling that one would find in men whose training, or lack of it, is not expected to help them control their emotions or to render impartial judgment on matters that come before them.

As the answers continued coming in, a great temptation presented itself to call this paper *The Psychological Reactions of Biologists*, but a calmer judgment prevailed.

Political, religious, educational and traditional boundaries are so much a part and parcel of the human individual that, try as he will, he can never avoid being influenced by them.

Here comes one letter filled with the bitterness of life by virtue of his country's partition, leaving but "an insignificant group of hillocks," as he puts it, which men now force him to call by the name of a country for centuries great and glorious.

He no longer feels he has a Fatherland. For him, his country has ceased to exist. There comes another breathing of hope and looking with patriotic enthusiasm to a wondrous future following the birth of a new Fatherland whose racial and national ambitions have had to lie dormant since time immemorial.

Let us first note in what specific fields of biological endeavor the majority of experimenters have been working during our generation, and what it was that gave the impetus to such work.

GEOGRAPHY AND BIOLOGICAL INTERESTS

While all nations have many men employed in various departments there are nevertheless certain more or less specific fields in which the majority of the workers of any specific country find themselves primarily interested, this being due to geographical conditions rather than to political boundaries. For instance, one finds Canada and the Scandinavian lands with vast coast lines always interested in fisheries and all that relates to them. But we shall let the Norwegian biologist, Hjalmar Broch, speak for himself:

A survey of the biological work in Norway in many respects shows that geographical conditions play a predominant part. On the one hand we are situated in the periphery, and we see how "modes" prevail in theoretical studies. During the first years of the century the cytological mania, which had already culminated in Central Europe, also made its way to our university, and gradually faded away again some time after it had played out its predominant part in Germany. Then studies of heredity made their way northward, and are at present *à la mode* to a degree that every student of biology finds it his duty to bestow a tinge of this on his theme however far the latter in reality may be apart from the field of heredity investigations. In many cases we can trace this mania backward to the rise of certain leaders of little originality who wish to be *à la mode*, so as to get a place among the real leaders of the epoch.

There is, however, one field of biology that runs like a real thread through the history of Norwegian

biological science—the ocean. From the earliest times our nation has been a nation of sailors and fishermen, and it was from the beginning but natural that the attention of Norwegian biologists should also be roused by the sea, the country having a coastal line of more than 3000 kilometers, whereas its breadth is in most parts quite small.

The great traditions given by such zoologists as Johan Ernst Gunnerus, Michael Sars, and Georg Ossian Sars, have naturally put their stamp on Norwegian biology, and therefore the most important biological contributions are naturally connected with marine research.

Likewise in Canada, considering biology as it applies to economics and industry, we find that the most important effort mentioned is that of the coöperative development by the Canadian universities of economic fisheries research, including the formation of the Biological Board of Canada, and the establishment of marine laboratories. There is Saunders' work on Marquis wheat, which has made "millions for Canada," and better still, it has created the atmosphere of economic adjustment of plants and animals to northern environments. The production of Marquis wheat, a pure example of the older selective breeding, was the direct response of a practical minded man to solve a particular Canadian or northern American problem of high yield and short season.

In the United States and in other countries, where many new types of plants have been imported, an international exchange of both useful and deleterious insects has been made. Entomological work of ascertaining "which is which" and trying to bring back that much needed balance in nature which keeps plants in good health and growth, also has been pursued. Many insect pests flourish in their new homes because those particularly predaceous and parasitic insect enemies which ordinarily keep them in check are not imported with them. But an interesting work has grown up in finding what

these insect enemies are and importing them.

In connection with work of this nature, one can show how some of the larger animals may be, and are, conserved by international coöperation. Vernon Kellogg calls attention to the fur seals of the Pacific, which were rapidly approaching extinction on account of unrestricted killing on the high seas as well as on their breeding grounds in the Pribilof Islands, when international agreements made in 1911 among Great Britain, Russia, Japan, and the United States saved them as a species and at the same time allowed a reasonable taking of skins.

This geographical aspect is also prominent in the report of the 1926 meeting of French scientists. Owing to economic conditions the Colonies must be developed. President Alfred Lacroix particularly stressed the part that science must play in the development of Tunis, Algeria, Morocco, Senegal-Niger, Guinea, the Congo, Indo-China, and other regions under French control. In fact, that year's meeting of the French association was held in Constantin, Algeria. Even Dr. Voronoff, the gland surgeon, has passed from human gland transplantations to work on farm animals, with a view toward producing heavier sheep bearing more wool. And Australia, a very few years back, spent something like \$600 per man to bring a group of scientists to its shores, hoping that some of her own particular problems would and could thus be solved.

Nearly all biologists consulted thought that the economic side of their science was of considerable, though by no means of greatest importance, and by this term some included everything in the way of human relationships. In fact, the term "human biology" is used by several, referring to the relations of man to his environment, that is, to the way biology is applied to

economics, to medicine, to education, to sociology, and to psychology.

In the United States biological workers have been employed probably chiefly in experimental general biology, in genetics, in embryology, in cytology, in tissue culture, and in general physiology.

In genetics the impetus came through the work of Mendel, Weismann and Roux in European countries, and in the United States through that of Wilson and Morgan.

J. Stanley Gardiner, of Cambridge, holds that history fertilizes the scientific soil, and that there is a considerable correlation of science with any profound disturbances which cover wide areas. Thus

China for 6000 years has altered very little and shows little advance. Our great advances in Europe are correlated with (1) the dominance of Spain and the profound wars in the 16th century; (2) the Cromwellian and other troubles in Europe of the 17th and early 18th centuries; (3) the Napoleonic times was a great advance; (4) 1850 with its revolutions or attempted revolutions, and (5) the last 20 years has been a time of great unsettlement and difficulty; where we are going now, I do not know; I expect we are in the stodgy period, but in 40 or 50 years we may have a world cataclysm which will stimulate people afresh.

A general survey of the literature on biology of the past thirty years demonstrates that the earliest investigators by no means always had enough facts at hand on which to build their speculations, but one may add that such lack of facts by no means lessened the output of speculation. However, an amount of good work was done, so that one really did obtain more exact anatomical and physiological data, especially in cytology and neurology. Much of the advance in the latter subject was due to the excellent work of the Spaniard, Ramon y Cajal. Considerable promotion and dissemination of biological knowledge through various periodicals then took place, which in turn stimulated general interest enough so that provision

was made for specially equipped laboratories.

But merely extending knowledge a step further is not developing science. Breeding homing pigeons that could cover a given space with ever increasing rapidity did not give us the laws of telegraphy, nor did breeding faster horses bring us the steam locomotive. The so-called improvements of the microscope pertain to improving the stands rather than the lenses. Until a new principle of optics is discovered the microscope remains what it is.

One can say of other fields of work what the late E. W. Scripps said of the ocean, "Why, of course, everything anybody can learn by investigating the ocean and the organisms that live in it will be useful to somebody in some way, sometime." But the real advance in science does not come from merely extending what we have, but very often from uncovering a slightly hidden something that we are permitted to use, and to work out some general law or principle from this. The problem is not, as Morgan says, "to discover how many kinds of structures exist, but whether there are common principles that run through them all. If there are no such principles, then we are indeed headed toward chaos."

Applying this thought to his particular work, he continues:

Although we have not gone very far in our analysis there is encouragement to go on. If one takes the cell-division in all its diversity, we shall not get very far by studying all the many variations resulting from slight differences in the structure of eggs of every species, but we shall really have succeeded in accomplishing something worth while if we find a few simple physical *principles* involved in that cell-division.

And so, too, one must not place credit for any given finding in the wrong place. Several writers of note have pointed out

that chattel slavery was quite necessary in one state of civilization if men were to make any progress and have any assurance of even an immediate success in their varied efforts. Then, too, it was not abolished because humanitarianism abhorred it, but because another type of civilization was brought about by the invention of the steam engine, which made it possible to sustain civilization without slavery. So, too, modern democracy did not evolve from any interest in the brotherhood of man, but because discovery and exploration opened up entirely new channels into which men's lives could flow and lead an independent and self reliant existence.

Now let us examine the biological literature and the letters received to see what the biological world considers important. One is struck immediately by the practical agreement of the biologists of all nations as to what is important and what has been done, during the past quarter of a century, that is of lasting value.

MENDELISM

One finds that after almost a half century of experimentation with just one idea in mind—of finding new angles by which to demonstrate evolution—a sigh of relief went up that other fields had finally been opened. Yet paradoxical as it may seem, the finding of the very factors which opened new fields had its rise in the discovery, or rather rediscovery, of a piece of work which in turn was the cause of producing another theory of evolution, namely, De Vries' theory of mutation. The rediscovery and verification came about, simultaneously, by De Vries in Holland, Correns in Germany, and Tschermak in Austria. These men gave to this generation a knowledge of an outstanding piece of work—a work consisting of

many experiments carefully performed and carried on throughout a great length of time by Johann Gregor Mendel. Mendel's work was actually done in a preceding generation, but as it remained unknown until our own, and as it has exercised the profoundest influence on all biological work since 1900, it deserves a place in this survey.

Mendel pointed out that definite numerical results were to be obtained in crossing peas, which he explained by two simple hypotheses—that of segregation and that of independent assortment.

The first of these is now accepted as a 'law' having a very wide application. All later discoveries in the field of heredity and genetics rest upon that law. It is, as Morgan says, "a broad generalization based on numerical data and allows us to predict with accuracy the outcome of a given solution."

Practically all these biologists whose opinion was asked were unanimous in putting the experimental work on genetics and heredity in the foremost rank of this generation's achievement.

Mendel's second hypothesis applied only within certain limits that can be accurately stated, but both hypotheses hold very definitely for the cases he studied and for characters of the majority of plants and animals studied since then. However, much knowledge has been added, in the way of additional facts, so that we now speak of a 'linking' and a 'crossing-over' of certain characters and with such equipment added, we apply the laws over a much wider field than Mendel did or could.

Much of the difficulty of early workers in any new field is that they are unable to formulate a question so as to get an intelligent answer, and much of the objection and faultfinding regarding Mendelism is probably due to this same fact.

ENTWICKLUNGSMECHANIK

Any new idea thrown into the biological arena would not only cause great numbers of men to follow experimentally the lead thus given, but the lesser leaders would be inclined to break into new paths also, though usually into closely related fields. So we find papers on genetics and heredity with emphasis on variation appearing one after another, and almost simultaneously, others on behavior and physiology. This work on physiology concerned itself primarily with the reactions of mature organs, and did excellent work for "medicine." A little later others drove the problem further back and the question of how the organism arose in the first place was given a niche in the gallery of experimentation. However, this beginning of embryology was largely descriptive, accounts being written merely of what was seen. From this descriptive work, in turn, real experimental embryology was born. Now men such as William Roux and Hans Driesch began destroying or removing parts of the early embryo to ascertain what would happen.

Roux's single pioneer experiment of note consisted in killing one of the first two cells of the dividing egg of a frog. The remaining half produced only a half embryo. Driesch, on the other hand, found that with one half egg of a sea urchin destroyed, the remaining half developed into an entire organism. Driesch finally showed that the apparent difficulty lay in the physics of the various eggs used for the experiment. In some cases the usual method of egg division caused one portion to be heavier than another and thus to sink into the surrounding nourishment. When the heavier part was removed, the lighter portion received but little or no nourishment, and consequently could not develop. If, however, one used an egg such as that

of the sea urchin or even of the frog and placed it so that nourishment was forthcoming, then each portion of the egg would result in a completely formed, but often somewhat smaller, animal.

Driesch finally came to the conclusion that to him at least, there was always something over and above what the laboratory could find in the development of a complete organism from such separate parts. He and his followers therefore took the stand that satisfactory explanations are more likely to come from an investigation of the essence of life than from any purely embryological and physiological experimentation in the laboratory.

PHYSIOLOGY

Here was a parting of the ways. Many sought to retrace their steps and to start anew. Thus some became interested in behavior, and from behavior of the entire higher organisms, or parts of those organisms, there was the inevitable tendency to go farther and farther back. If all life was but the working out of actions and reactions of masses of cells, and cells in turn were composed of protoplasm, it was but logical that one should study protoplasm. This was not only a fruitful field for an analysis both physically and chemically of the substance of protoplasm itself, but of the behavior of the single celled plants and animals, which being actual living organisms, must have within their single cell the answer to the riddle of life.

Physics had won first place in the sciences for four reasons: (1) it accepted the uniformity of nature, (2) it insisted upon exact measurements, (3) it concentrated attention on the regularities that underlie the complexities of phenomena as they appear to us, and (4) it emphasized the importance of crucial experiments.

It was but natural that physiology should try to do with organs what physics

did with inanimate material. Thus the study of mere reactions came into being, so that first we wanted to find out the actual chemical make-up of the material with which we were working and then how it would react to all manner of stimuli as a whole, as when, for instance, certain portions were eliminated. From the grosser experiments there was a resort to finer ones, and here a single organism was taken and subjected to all manner of "indignities" to see how this particular thing would react under very particular and definite excitations. But again, biological workers landed in the same type of *cul-de-sac* in which Driesch had landed.

As J. Arthur Thomson says

the chemical-physical formulations do not actually describe what we see and know. If complete they would afford a ledger of all the chemical and physical transactions that go on in the body, but that would not describe the organism's apparently unique qualities as in integrated living individuality, such as the power of enregistering its experiences within itself so that subsequent behavior is influenced. As science is at present it is necessary to use special biological categories describing the life of the organism—notably its growing, reproducing, developing, varying, endeavoring. For isolated transactions in corners of the body, the chemical-physical description may suffice, but not at present for anything like behavior.

THE GENE

Let us retrace our steps for the moment to the birthday of a single little fruit fly in 1910, which happened to be born with white eyes. We find this seemingly insignificant animal the chief factor in furnishing an impetus toward a study of heredity and genetics, which has brought forth what many biologists consider the nearest approach to the solution of any biological problem yet presented.

The impetus this solitary fruit fly gave to the study of heredity and genetics has brought us to the belief that each chromosome is made up, in turn, of a chain of

separate particles which we call "genes," because it seems that they are the very basis on which the genealogy of the individual rests.

Maybe each chromosome has thousands of these genes, and probably no two are alike. The individual plant or animal is the product of the activity of all the genes together, while heredity is the result of the shuffling of these genes in each generation.

Quoting T. H. Morgan, who is the outstanding American in this field of work:

In several plants and animals we can refer these genes to particular chromosomes, and in one animal at least, about four hundred genes have been placed. On the assumption of their relative positions with respect to one another, we can predict what the numerical results will be in inheritance for some four hundred different characters. The theory justifies itself in that it allows one to predict the outcome in terms of numbers for all these four hundred characters whose genes have been located.

The genes divide when the chromosomes divide, and collectively their division is what we see when each chromosomal rod splits throughout its length. It is the genes that come together with extraordinary precision, which implies probably that we are dealing with events of a molecular order. We can go no further until physics has furnished us with a key to unlock these extraordinary events.

Boveri's work on the mechanics of cytology must not be left unmentioned at this point.

So far we have discussed the work on cytology, genetics, and heredity, embryology and regeneration, and physiology with its subheadings of physics and chemistry. One should not forget the exceptionally interesting and valuable work on tissue cultures outside the body of the individual in which they originally grew, done by Ross G. Harrison and Alexis Carrel. These men were able to take individual cells and groups of cells and keep them alive and in apparently good health quite outside of their usual habitat.

The work on the possibility of artificial

parthenogenesis by Yves Delage and Jacques Loeb also belongs in this field. A mere pricking of the frog's egg with the point of a glass or platinum needle and then washing the eggs in blood, will produce fatherless frogs. In other cases a chemical or physical change of the water in which the eggs are placed will cause unfertile eggs to develop.

Baltzer's work with the green worm of the Mediterranean and the North Seas seems to show that sex may be determined by either environment or food, or a combination of both, for he was able to produce intermediate sexes by merely shaking, from their usual position, those which would ordinarily have become males, and forcing them to grow in a foreign medium.

The work of H. S. Jennings on the behavior of the lower organisms seems to demonstrate some "purposive behavior" even in animals of a very low level. Such experimental work as having a brainless starfish attack and conquer an equally brainless, but none the less formidable, sea urchin may throw much light on some future experimental psychology.

Closely akin to this type of experimentation is that of the various "tropisms"—the name given to those "ingrained constitutional obligations to adjust the body so that the two sides, perhaps the two eyes, ears, or nostrils, are equally stimulated" to secure a physiological equilibrium.

Thus the young eel or elver goes straight upstream, the male mosquito finds the buzzing female, and the moth flies into the unnatural stimulus of the candle. Somewhat higher is the persistent way in which newly hatched loggerhead turtles make for the open horizon, as Professor G. H. Parker has shown, which usually and happily means finding the sea.

Finally, one may add the work done in comparative psychology, and the attempt to show what effect the "mental" has had in determining the path of evolution.

In this connection also, should be men-

tioned the work of Robert Chambers in developing a technique of microscopic dissection, which opens up a field yet unexplored, and that of Professor Pregl of Graz, who has done outstanding work on the ultramicroscope and developed new methods in microanalysis.

From an agricultural point of view, a valuable answer has been found for such questions as, "How can we, even by an importation of many different types of plants and animals, each susceptible to differences in temperature, climate, soil, moisture, and disease, keep that particular balance in nature which modern transportation is continually upsetting, by importing with such plants and animals those particular parasites, which will keep or again bring back that particular balance in nature so much needed"—by the workers in applied entomology well represented by such a man as L. O. Howard, who has furnished some of our most stimulating answers.

VITAMINS

In biochemistry, the paper of Hopkins and Willcock *Amino Acids in Metabolism*, in 1907, foreshadowed the very important discovery of vitamins. Here it is shown that there are accessory food factors in the growth of an organism which cannot be chemically analyzed.

Indirectly correlated with this field in its scientific aspects is the work of Dr. Allen on the *Artificial Culture of Marine Plankton Organisms*. His study showed that organisms, when developed artificially, require that chemically pure solutions be sensitized by natural waters before they can live and breed in them.

The work on vitamins, the discovery of their production in relation with sunlight, etc., is of great concern not only to the health of man, but of considerable prac-

tical utility in connection with the production of his food supplies.

Under biochemistry one should certainly mention what J. Arthur Thomson considers one of the great milestones in biology—the discovery of a "glutathione" by Sir F. Gowland Hopkins in 1921. This is an organic substance widely distributed in plant and animal cells, which acts as an "oxygen transporter," that is, as an intermediary between the oxygen of the air and the food-materials of the tissues. Its biological importance is due to the fact that "this transporter and liberator of oxygen accounts for the energy-yielding combustions that take place at a low temperature within the living cell. It explains how the cell burns and yet is not consumed."

D. Keilin's discovery of the cell-pigment "cytochrome," which has something to do with the control of oxygen within the cell, should also be mentioned.

Finally, Professor Baly's discovery of artificial photosynthesis should not be forgotten. Baly's work made possible the forming of organic compounds such as formaldehyde from water and carbon dioxide, which process, in turn, formed sugar.

Nearly all biologists placed the work on endocrines as among the most notable achievements of this generation. Thomson says of these so-powerful factors in the lives of all organisms that they are chemical messengers which are like "keys that open certain doors and close others, and they exert a regulative action on many of the functions of the body, securing their orchestration or correlation."

The discovery of this chemical integration

has changed the whole face of physiology. Biologically regarded, the hormones, such as adrenalin and thyroxin, enable the biologist to understand not only everyday events such as the cat's hair standing on end

before the intruding dog, but the changes that come in adolescence when hormones from the reproductive organs saturate throughout the body, and activate the growth of the stag's antlers, the swelling of the frog's first finger, and scores of other adolescent novelties.

MEDICAL BIOLOGY

The most spectacular work in preventive medicine, which really belongs in this century because real effective proof of its working out was not forthcoming until 1900 or thereafter, is that of the discovery of how malaria and yellow fever are carried, followed by the exceptionally effective methods used in applying this knowledge in those regions where the disease was ever a source of dread and death. It was a Latin American, Carlos Finlay, who was really the pioneer in yellow fever work and a Brazilian, Oswaldo Cruz, who saved the lives of untold millions by his intelligent application of the principles that Finlay and Reed discovered.

One might add the discovery of diphtheritic antitoxin to the list of outstanding medical discoveries that were ushered in at the moment when the nineteenth century was giving way to the twentieth. No longer ago than 1893, where records were kept, some 58 out of every 100 diphtheria cases ended in death. After 1895, with the discovery of antitoxin, there were less than four deaths in every hundred diphtheria cases, provided, of course, that the antitoxin was injected shortly after the onset of the disease.

With typhoid fever, the change in fatalities is even more startling. During the Boer War (1899-1900) with only approximately 208,000 soldiers engaged, there were 57,683 cases of typhoid with 8,022 deaths, while only 7,781 men were actually killed in battle.

Only sixteen years later among the British on the great Western Front during

the World War, with approximately 1,300,000 men, there were in all only 7,500 typhoid cases of which 266 resulted in death. This typhoid comparison is of especial interest because the French did not use the methods employed by the English during the first sixteen months of the war, with the result that their reports show 96,000 cases of the disease with 12,000 fatalities.

One should mention here, also, the discovery of insulin by Banting, which is of far reaching medical import. The story of this piece of research, which ultimately culminated in the discovery of insulin, according to a correspondent had

a long background of trials as between the known facts of sugar reduction in the body, the immediate necessities of diabetic patients, the existence of corrective substances in the pancreatic secretion and above all the clinical failure of gross pancreatic secretion. It was the idea of utilizing pancreatic material before the normal external secreting cells had developed in the young, coupled with some highly practical knowledge of domesticated animals that gave Banting his opportunity.

F. D'Herelle's discovery of the bacteriophage, the enemy of germs, a "parasite upon a parasite" and not a chemical something, also is considered of great possible importance for the future. Then, too, the extremely important and almost exhaustive researches of Maud Slye upon over 50,000 mice have demonstrated at least one thing in regard to cancer—that both resistance and susceptibility to that dread disease are hereditary in the animals studied.

UNSOLVED PROBLEMS

With this little summary of the outstanding biological work of our own generation, we may pass on to what problems the biologists themselves feel have been actually solved during this period and try to ascertain what they consider the most important problems still unsolved.

All are agreed that no problem has been fully solved, but that, nevertheless, much light has been thrown upon a good many points of interest which will prove valuable for workers of the future, in continuing from where we of this generation have left off.

It may afford the layman an interesting insight into the mind and thought of the biologist to read a letter such as this:

You ask my opinion as to the most important biological problems of our age! I must confess that I find it utterly difficult to give an exact answer. Any biological problem is of importance, none is superfluous or even of subordinate importance (that is, if you think of biology as a whole and not only as an aid to industry, etc.). Biology is a building that needs every one of its stones—if you take any one of them away the entire building will fall into pieces again. Every biological investigation is of equal importance; i.e., if it is not worked out or followed out into caricature. Only history can in the long run decide and estimate with certainty the sound kernel of each "mode"—every "mode" is bound to be driven in caricature, when its adorers take the last steps into that *cul-de-sac*, where every mania sooner or later comes to an end. Choose whichever instance you will, systematics and classification, phylogeny, cytology, physiology, heredity, etc.—you will, in every case, find that students of biology at last put their heads into the *cul de sac* and cannot get further until they are pulled out by some other partial discipline. The side path was passed by unheeded, because they could not and cannot look in more than a single direction—most biologists have only small horizons. To every age, the problem or problems will seem to be of greatest importance where some of the great personalities of that special epoch casually are leading others.

More than one writer speaks of the "fads and fancies," which have taken hold in biology at various times, and these men call attention to the fact that we have but to examine the scientific journals to see the successive waves of contributions on tropisms, artificial parthenogenesis, cytology, spermatogenesis, regeneration, genetics, tissue culture, endocrines, etc., which have come and gone. There seems to be some one stimulus for such work, which

springs from some particular discovery that promises a way out of the mechanistic dilemma, that is, which promises some light on a mechanistic explanation of living phenomena. Many then start work on a problem and pile up apparently stronger evidence, only to find themselves at sea more than they were before. That particular discovery is then dropped, and work is begun on another, followed by the same result. This procedure necessitates intensive work which leads to quick results, and has its advantages, of course, but instead of following a problem out with some degree of finality, it is given up and another fad is followed.

Back of all experimentation the impetus seems to come from a belief that in the physico-chemical explanation lies the only mode of approach to an understanding of life itself, acceptable to modern man.

Let us then, at this point, try to find what modern biologists consider the most fundamental problems of the day.

Again there is practical unanimity.

(1) The nature of life. That is, does living organic substance differ from the inorganic? While this problem is far from being solved, it seems that the recent work on bacteriophages and the filterable viruses is pushing our horizon to a much lower level.

(2) The discovery of the constitution of protoplasm and its manner of operation.

(3) The problem of the causes of variation, which may in turn be stated as the mechanism of differentiation and the mechanism of evolution.

(4) Cancer research. Cancer is ravaging humanity continually to a greater extent, and practically nothing is known of either its origin, its control, or its cure.

(5) The relation of genetics and environment. Important because so many human problems are affected by genetics, such as disease, sociology, etc.

(6) Disease. Is its predisposition really hereditary, or is it environmental? Is any defect really hereditary or is it induced by environment?

(7) Criminality. Is it hereditary, or is it environmental in its origin? These are decidedly important human problems. Even immigration is affected by the answer.

(8) So-called superior and inferior peoples or races. Are they really such?

(9) Economic entomology. Particularly emphasized because of the growing importance of many species of insects. The interference with the balance of nature converts many insects into potential or actual enemies of man and his products. An enormous amount of work needs to be done in this field.

All agree that the work done on genetics and heredity and in the related fields of physiology and biochemistry has greatly extended man's knowledge of the mechanism of inheritance and the relation of inheritable units to definitive characters resulting in the development of the organism. They also agree that they have thrown considerable light on sex differences and the determination of sex, while the work on the ductless glands has thrown a light on personality and human biology. But these studies also cause us to withdraw our former idea that heredity was everything and environment nothing.

What has really been demonstrated by this work may be summarized as follows:

(1) That heredity is an orderly process, obeying certain very definite laws.

(2) That environment is coequal with heredity. What part each plays is still to be solved, that is, in any given instance *something may be the product of environment or of heredity, but the question of which is the more important can be studied only in the individual case.*

(3) From the philosophical side, that genetics is the single experimental criterion of evolution, and hence of biological philosophy. Its findings have, therefore, forced the withdrawal of science from the welter of speculation into which it had

fallen, by establishing experimental tests for the various claims. And finally,

(4) That genetics permits a better valuation of so many problems of disease, of insanity, of feeble mindedness, and of various individual and social problems.

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NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of THE QUARTERLY REVIEW OF BIOLOGY, 1901 East Madison Street, Baltimore, Maryland, U. S. A.

BRIEF NOTICES

EVOLUTION

THE FUTURE OF THE EARTH.

By Harold Jeffreys.

W. W. Norton and Co., Inc.

\$1.00 4 $\frac{1}{8}$ x 6 $\frac{1}{2}$; 79 New York

A billion years ago, or so, a wandering star came within the gravitational field of the sun, and through the tidal forces set up, pulled out a long filament of gas. Under the gravitational attraction of its parts, the filament broke up into droplets which later condensed. These are the planets, and one of them is the earth, on which we move and have our being. Another mass was secondarily separated from the earth by the sun and this is our moon. From those early times till now, the temperature on the earth has been fairly constant, with intermittent fluctuations, but in the future things will be colder. The earth obtains almost all its heat from the sun, and the latter as a reservoir is being depleted at an enormous rate; so much so that in another billion years, the ocean will be frozen even at the equator. In the meantime changes will be in process in the relation of the earth and its moon. The tidal forces between these two operated at first to slacken

the speed of the earth's rotation and increase the moon's distance. This will continue until the period of rotation of the earth and revolution of the moon are equal to about 45 days. After that the sun will take an upper hand over the moon in its tidal influence on the earth. It will slow the earth still further and the moon will again approach. Then these two will collide.



THE UNIVERSE AROUND US.

By Sir James Jeans. The Macmillan Co.

\$4.50 5 $\frac{3}{4}$ x 8 $\frac{1}{2}$; x + 341 New York

This is one of the more successful of the attempts to present popularly the results of recent advances in physical science. It has been a best seller and deservedly so. Written primarily from the viewpoint of the pure astronomer, it nevertheless does not confine itself to consideration of heavenly bodies. The whole range of physical theory regarding space and matter from the infinitesimally small to the infinitely large is surveyed with beautiful clarity and vividness. In speculative matters the author tends to a pessimistic outlook. Where alternative theories are available,

he prefers the picture of a universe running down constantly and inevitably to a dead level of unavailable energy.

The complaint has been made that in his writings on the origin of the solar system, Jeans has not given sufficient credit to the American contributors to the tidal theory. The charge seems to be substantiated in this volume. Neither Chamberlin nor Moulton is mentioned in the index.



THE STORY OF EVOLUTION. *Facts and Theories on the Development of Life.*

By Benjamin C. Gruenberg.

D. Van Nostrand Co., Inc.

\$4.00 6 x 8½; xvi + 473 New York

Dr. Gruenberg has already established a secure reputation as a writer of really sound elementary texts and popular expositions of biology. The present volume will enhance this reputation. It is a sane, well-balanced, entertainingly written, and adequately illustrated popular account of the present state of knowledge about organic evolution and the chief factors which have been concerned in it. It should make an excellent college text, as well as a sound guide to the general reader who wishes to learn, without too great effort, how far along biologists have got with the problem of evolution.



WHEN MAMMOTHS ROAMED THE FROZEN EARTH.

By Heinrich Schutz. Translated from the German by Frank Barnes.

Jonathan Cape and Harrison Smith

\$2.50 5½ x 8½; 197 New York

A book for young people picturing what the author conceives to have been the trend of events during the closing era of the glacial period. He tells of terrific storms, of fierce animals roaming the earth and

battling with one another, of the downfall of the mammoth and the rise of man. Altogether he has a yeasty imagination. The book is more or less thrilling in spots. It perhaps suggests as true an account of what happened in that far off age as it is possible to attain after a lapse of many thousands of years, since it is impossible to check the imagination, except occasionally in regard to a minor detail, in regard to which there are some obvious slips.



JURASSIC FOSSILS FROM JUBALAND, EAST AFRICA, COLLECTED BY V. G. GLENDAY, and the Jurassic Geology of Somaliland. *Monographs of the Geological Department of the Hunterian Museum, Glasgow University, III.*

By J. Weir (with descriptions of Echinoidea by Esthel D. Currie, and of Corals by Mary Latham).

Jackson, Wylie and Co.

12 s. 6d. 9½ x 12½; 63 + 5 plates Glasgow

This monograph contains the following sections: "The Jurassic geology of British Somaliland," "The geology of the Juba and Daua Rivers," "The Marehan Sandstone," "The palaeontology of the Jurassic Rocks described in Mr. Glenday's Report," "Description of the fossils—Mollusca, Brachiopoda, Echinoidea, and Corals," and a "List of the Fossils described." There is a list of 47 references and a group of excellent photographic plates.



NEW VIEWS ON EVOLUTION.

By George P. Conger. The Macmillan Co.

\$2.50 5½ x 7½; ix + 235 New York

This volume of the *Philosophy for the Layman* Series treats of the concept of evolution, not only in biology, but in physics, chemistry, geology, psychology and sociology. The conclusion reached

is that, while there is no decisive evidence against creationism, evolutionism is a valuable correlating principle.



THE EVOLUTION OF EARTH AND MAN.

By L. L. Woodruff, G. H. Parker, R. S. Lull, Charles Schuchert, H. B. Ferris, Joseph Barrell, A. G. Keller, G. G. MacCurdy, Ellsworth Huntington, J. R. Angell, E. G. Conklin, W. R. Coe. Edited, with a Preface, by George A. Baitsell.

Yale University Press

\$5.00 6 x 9; xv + 476 New Haven

This is a revised edition of *The Evolution of the Earth and Its Inhabitants* and *The Evolution of Man* combined into one volume. Two new chapters have been added: Cultural Evolution, by G. G. MacCurdy, and the Mechanism of Evolution, by W. R. Coe. These additions live up to the high standard of the original chapters.



DUST TO LIFE. *The Scientific Story of Creation.*

By Burton P. Thom. E. P. Dutton and Co.
\$5.00 5½ x 8½; xv + 409 New York

A popular account of evolution, which, after a couple of introductory chapters on cosmogeny, devotes itself with considerable thoroughness to a setting forth of the results of paleontology, ending with an account of the ascent of man. The book is entertainingly written, and abundantly illustrated with line drawings. It lacks any bibliography, but is well indexed.



ORGANIC EVOLUTION.

By Richard S. Lull. The Macmillan Co.
\$4.50 5½ x 8½; xix + 743 New York

A revised edition of a well known text book.

SECOND BIBLIOGRAPHY AND CATALOGUE OF THE FOSSIL VERTEBRATA OF NORTH AMERICA.

Carnegie Institution of Washington Publication No. 390, Vol. 1.

By O. P. Hay.

Carnegie Institution of Washington

\$7.50 (paper)

Washington

\$8.50 (cloth)

6¼ x 10; viii + 916

Supplementary to a similar volume issued in 1902, and covering the literature published subsequent to that dealt with in the first work.



GENETICS

BESTIMMUNG UND VERERBUNG DES GESCHLECHTS BEI TIEREN. *Handbuch der Vererbungswissenschaft, Lieferung 10.*

By Emil Witschi.

Gebrüder Borntraeger

10 marks (paper)

Berlin

20 marks (bound)

7 x 10½; 115

DAUERMODIFIKATIONEN. *Handbuch der Vererbungswissenschaft. Lieferung 11.*

By J. Hämmerling.

Gebrüder Borntraeger

6 marks (paper)

Berlin

12 marks (cloth)

7 x 10½; 69

These two new parts of the Baur-Hartmann handbook of genetics furnish useful summaries of the literature of sex determination in animals and permanent modifications of unicellular organisms. Witschi's contribution devotes approximately 100 pages to primary sex determination, under two main headings, genetic analysis, and the physiology of primary sex determination. Hämmerling reviews the literature of *Dauermodifikationen* in *Paramecium*, *Arcella*, *Gonium*, and a few other organ-

isms. Both parts carry extensive, though by no means exhaustive, bibliographies.



HEREDITY IN MAN.

By R. Ruggles Gates. *The Macmillan Co.*
\$6.00 5 $\frac{1}{8}$ x 8 $\frac{1}{4}$; xiii + 385 New York

This volume began as a new edition of Professor Gates' earlier book on heredity and eugenics, and ended as what practically amounts to a new and different book, under a new title. In its present form it is one of the most useful summaries of the present state of knowledge regarding human inheritance which has come to our attention. It covers the field systematically and thoroughly. The bibliography, arranged by subjects, chapter by chapter, is extensive, and complete enough for all practical purposes of a handbook. Professor Gates merits the congratulations of all students of human biology for the book.



BLOOD GROUPING IN RELATION TO CLINICAL AND LEGAL MEDICINE.

By Laurence H. Snyder

The Williams & Wilkins Co.
\$5.00 5 $\frac{7}{8}$ x 9; xi + 153 Baltimore

In this book are to be found all the important developments of the many phases of the problem of blood grouping. The author, who has had much practical experience in performing transfusions in addition to having been an experimentalist, particularly in the field of inheritance of blood groups, their racial distribution, and pathological and physiological conditions, is well fitted to prepare such a treatise. It will be highly useful to both the legal and medical profession and invaluable to the research worker. The volume contains numerous tables and diagrams, an extensive bibliography and an index.

GENERAL BIOLOGY

BIOLOGICAL PRINCIPLES. *A Critical Study.*

By J. H. Woodger. *Harcourt, Brace and Co.*
\$7.00 5 $\frac{3}{8}$ x 8 $\frac{1}{4}$; xii + 498 New York

There has been in the last fifteen years, largely as a result of developments in the new physics, a renaissance of interest in the philosophy of science, and to an important degree it affects the outlook of biology. The biologist can no longer take his fundamental viewpoint from the simple mechanism of the text book of physics, if for no other reason, because physicists have abandoned this view as inadequate to their own phenomena. Interestingly enough, the modification of the philosophy of mechanics is in the direction of an organic idealogy. There is a distinct need now, for a probing of biological fundamentals by biologists, to align their viewpoint with that of their fellows in the search of knowledge. Towards that end, the present work is a significant and welcome contribution. The author, who is a reader in biology in the University of London, painstakingly surveys *seriatim*, the various important philosophical viewpoints that affect biology, and critically examines their logical and epistemological content. His own views, some of which have been presented in *THE QUARTERLY REVIEW OF BIOLOGY*, are well worth considerable attention but lack of space will not permit an adequate statement of them. Suffice it to recommend the book as probably the best review extant of biological philosophy in its current important aspects.



L'ORDINE DEI TEMPI E DELLE FORME IN NATURA. *Introduzione allo Studio Generale delle Funzioni Periodiche. In two parts.*

By Vincenzo Capparelli. *Licinio Cappelli*

100 lire

7 x 10; Part I, 258 (paper)

Part II, 533 (paper)

This extensive and detailed critical review of what is known about cyclical phenomena in the biological realm is a valuable addition to general biological literature. The first volume is historical, and discusses the various theories of the rhythms and cycles which have been advanced by biologists, medical men, and philosophers. The second volume reviews the recent as well as the ancient literature of biology relative to such matters as seasonal periodicity of morbidity and mortality, growth, reproduction, etc. The treatise is well documented and illustrated. The lack of an index unfortunately impairs greatly its usefulness as a reference work.



OUTLINES OF MODERN BIOLOGY.

By Charles R. Plunkett.

Henry Holt and Co., Inc.

\$3.75 5½ x 8½; vii + 711 New York

This generation sees biologists who are no longer natural historians or morphologists representative of the older school but instead are chemists and physicists of living matter, albeit still teaching their subject largely from texts mostly based on the older discipline. It has not been uncommon for teachers of biology to regard their field as somehow being more difficult for students than that of other sciences, and possibly this impression is reflected by the less stimulating character of many collegiate texts published in the past. In the present work, however, the author's aggressive attitude toward modernizing collegiate biology is expressed by his statement that his book is no more difficult than modern college textbooks of physics and chemistry, and that he perceives no good reason why they should be less so,

Bologna

in view of the greater inherent complexity of the subject matter of biology. Progressive teachers of biology will unquestionably be in sympathy with this attitude.

Dr. Plunkett builds his book around the concept of the living organism as a physico-chemical mechanism, the emphasis being on general principles rather than on the factual details one associates with a text written from the basis of the type system. The initial theme of protoplasm is amplified into sections dealing with the comparative physiology of plants and animals under the headings of nutrition, response, reproduction, and evolution. The many still unanswered questions of biology are not ignored but viewed as stimulating problems rather than discouraging mysteries. A thoughtful chapter on the origin and nature of life concludes the volume, while his last statement crystallizes the central problem of biology today—that the essential "secret of life" lies in the genes themselves; their composition and structure, how they are autocatalytically synthesized, and how they may have first originated from lifeless matter.

Not only has the author given us a useful and tested text but it is highly probable that it is pioneer to others of similar but more detailed plan. It is to be especially recommended for the use of students who have had some previous training in science.



LES ULTRAVIRUS ET LES FORMES FILTRANTES DES MICROBES.

By Paul Hauduroy.

Masson et Cie

40 francs 6½ x 9½; 392 (paper) Paris

Bacteriologists should all be grateful to Dr. Hauduroy for getting together in one place an enormous amount of information on a subject which is now an exceedingly important and interesting one. One hundred and fifty-five titles are listed in the

bibliography and many more are scattered throughout the text. Hauduroy discusses the ultraviruses which attack not only man but plants, bacteria, insects, fishes, birds, and mammals. He discusses the recent discoveries which make it appear almost certain that there is a filtrable form of the virus of tuberculosis. The book is well written and the material is arranged in an orderly way. It should make a valuable addition to the library of every bacteriologist.



MY TROPICAL AIR CASTLE. *Nature Studies in Panama.*

By Frank M. Chapman.

D. Appleton and Co.

\$5.00 $5\frac{3}{4} \times 8\frac{3}{4}$; xv + 415 New York

This is an extremely interesting and entertaining book about Barro Colorado, an island in Gatun Lake in the Panama Canal Zone, and the research laboratory on it. While written primarily for the general public every biologist, whether he has worked at Barro Colorado or hasn't, will enjoy reading it. Naturally the avian fauna gets the major part of the space, but no part of the extraordinarily rich life of the island is wholly neglected. The volume is extensively and beautifully illustrated by photographs and drawings. It is popular natural history at its very best.



HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 309. Methoden der Süßwasserbiologie.* Containing following articles: *Anleitung zur Untersuchung des Limnoneustons*, by W. M. Rylov; *Haltung und Aufzucht von Süßwasserbryozoen*, by Heinz Graupner; *Die Zucht des Phytoplanktons*, *Die Zucht von Cladoceren, eines Ostracodens, von Copepoden*

und planktischen Rotatorien, and *Die Zucht des Aufwuchses unter Anwendung der Methode des Aufwuchsträgers*, by Einar Naumann; *Methoden der teichwirtschaftlichen Versuchsanstellung*, by Reinhard Demoll and Emil Walter; *Die Messung des Eindringens von Licht in Wasser mit photoelektrischen Zellen*, by V. E. Shelford; *Methoden zur Untersuchung von Flusslebensgemeinschaften*, by V. E. Shelford and Samuel Eddy.

Urban und Schwarzenberg

9 marks 7×10 ; 165 (paper) Berlin

This number of the Abderhalden Handbook deals with methods of fresh water biology. Among the most generally interesting of the papers are those of Rylov on the organisms of the surface scum of stagnant pools, of Shelford on the measurement of the penetration of light into water, and of Shelford and Eddy on the ecology of rivers.



NATURE NARRATIVES. *Volume I.*

By Austin H. Clark.

The Williams & Wilkins Co.

\$1.00 $4\frac{7}{8} \times 7\frac{1}{2}$; viii + 135 Baltimore

Dr. Clark has the great advantage over many of his fellow popularizers of science of knowing what he is talking about. These articles, originally written for a newspaper syndicate, are convincing evidence that accuracy and picturesqueness are not necessarily incompatible.



BACKGROUNDS OF BIOLOGY.

By John Giesen and Thomas L. Malumphy.

The Bruce Publishing Co.

\$2.50 $5\frac{1}{2} \times 8\frac{3}{4}$; x + 278 Milwaukee

Two professors in a Roman Catholic college give in this book an introduction to biology for those students who have not time for a more extended course. In their treatment of evolution they are careful to

give the Darwinian dogs the worst of the argument.



INSTRUCTIONAL TESTS IN BIOLOGY.

Comprising Twenty-five Tests in Animal, Human, and Plant Biology for Junior and Senior High Schools.

By J. G. Blaisdell. World Book Co.
32 cents Yonkers-on-Hudson, N. Y.

6 x 10; viii + 56 (paper)



HUMAN BIOLOGY

QUESTIONED DOCUMENTS. *Second Edition.*

By Albert S. Osborn (with an Introduction by Prof. John Henry Wigmore).

The Boyd Printing Co.

\$12.50 6½ x 9½; xxiv + 1028 Albany

The author of this stately and beautifully printed volume is an outstanding expert on handwriting, and, in this revised edition of what has long been a standard treatise, has produced probably the best work on the subject now in existence. As the title indicates the primary viewpoint is legalistic, that of the handwriting expert in the courtroom. But this point of view, because of its very detachment, probably adds to rather than detracts from the usefulness and interest of the book to the human biologist. Handwriting has been far too much neglected by the human biologists in general, and the anthropologists and psychologists in particular. They have left the field too much to quacks and charlatans. The handwriting of an individual is a highly stable, objective and quantitatively measurable personal characteristic, which, in a sense, integrates a whole series of extremely delicate and complex individual differences in the physiology of nerve and muscle.

In this volume Mr. Osborn furnishes a

sound, clear, and detailed basis for anyone who is interested in the scientific study of handwriting. He has devised measuring instruments adapted to such study, and has thoroughly done a lot of the inevitably necessary spade work which must underlie every really scientific approach to the problems of handwriting. His book is itself, in the highest sense, a scientific treatise. In an earlier work, *The Problem of Proof*, which, by the way, every scientific man will find interesting and valuable reading, Mr. Osborn made clear his possession of the scientific mentality and outlook. The present book should be in every anthropological, psychological, and, indeed, general biological library. It is extensively illustrated, meticulously documented, and indexed in detail.



ETHNOGRAPHY.

By Loomis Havemeyer. Ginn and Co.

\$4.80 6 x 9½; vi + 522 Boston

This is a compilation of ethnographic material, from well known sources, for use as an elementary text. The author specifically disclaims any originality of material. Sixteen chapters of the book were privately printed ten years ago, and have been used successfully in the author's classes at Yale since. There are five general sections, dealing respectively with the black, brown, red, yellow, and white races. Blacks and reds get the bulk of the space. Under the yellow race only Tibetans and Yakuts are discussed, and under the white race only Hindus. The author excuses the obviously large omissions on the ground that there is not space enough in an elementary text of this sort to treat all divisions of mankind. The author states that the book

is supposed to supply a set of facts drawn from the most reliable sources upon which the development of

a science of society may rest. I have excluded everything that is not a matter of agreement on the part of nearly all competent authorities. These facts I have not attempted to interpret, leaving matters of that sort to the discretion of the reader.

The book is abundantly and well illustrated, and within its self-imposed limitations is an excellent textbook for college and university classes.



THE DAWN OF A NEW CIVILIZATION.

By *Hardy Wilson*.

Cecil Palmer

7 s. 6 d.

5 x 7 $\frac{3}{8}$; 288

London

This curious book, cast in the guise of fiction, and in manner falling somewhere between the *Education of Henry Adams* and H. G. Wells at his theological worst, makes a highly futile Australian architect travel about the world and be dissatisfied with architecture and art in general. The basic thesis appears to be to the effect that

All signs show that we have arrived at one of those great changes when mankind moves from one period of creativeness, which has come to an end, towards another, which has not yet appeared. This period of transition means trials and failures before success is accomplished. The desire for creativeness is universal.

So far as is known creative men, in all ages, never were more than a few, and their lead was followed because of an instinctive desire to follow creativeness which affects everything about a race. Throughout periods of history it was a ruling force, and now it has reached, or is reaching, the end of a period, and so man turns to a new awakening. His creativeness always has occurred, in the first place, within that belt where the influence of the sun is dominant. Apparently, the perception of new creativeness is impossible outside of the belt, which is without white people who have energy and power to conceive a new period of civilization, unless it can be started in the southern United States, or Italians move southwards, and contact is established with China, or wherever inspiration may be found. As geographical position has been the determining factor in old moves, it is more likely that the United States will establish creative contact with the Chinese.

The book contains a dreadful libel on Richmond, Virginia, and some other odd information (?) about Maryland and Virginia, amongst which the following is a gem: "Jefferson Jackson's house, at Charlottesville, was a charming place too, and stood amongst leafy trees, smiling on a hill."



CRIME, DEGENERACY AND IMMIGRATION. *Their Interrelations and Inter-reactions.*

By *David A. Orebaugh*. *Richard G. Badger*

\$3.00 5 $\frac{1}{8}$ x 7 $\frac{1}{2}$; xvi + 272 Boston

The author says in the preface of this book that "a cursory perusal of the book will disclose to the most unsophisticated that it was not written for the scientist, or expert in criminology." Possibly that is the reason why he has such smooth sailing in defending the following points:

Degeneracy, a form of retrogressive evolution having its basis in evil heredity, predisposes to crime and may in fact be said to be its chief cause.

The extreme prevalence and increase of crime in America furnishes conclusive proof that degeneracy is widespread and increasing.

Crime and degeneracy as concurrent and mutually related phenomena in our social and civic life became unduly manifest and continued to increase both in volume and flagrancy contemporaneously with and in direct ratio to the immigration of low grade southern and eastern Europeans.

By the intermixture, both racially and socially, of the disharmonic and intellectually inferior element referred to with the old American stock, the racial blood-stream of the latter has been corrupted and degeneracy in varying degrees has supervened.

A consideration of all of the factors mentioned leads to the conclusion that the way to abolish or diminish crime is to eradicate degeneracy. The relation of crime to degeneracy, or degeneracy to immigration, and the reaction of each upon the other is readily discernible upon examination.



STUDIES IN THE NATURE OF CHARACTER. *By the Character Education In-*

quiry, Teachers College, Columbia University, in Coöperation with The Institute of Social and Religious Research. II. *Studies in Service and Self-Control.*

By Hugh Hartsborne, Mark A. May, and Julius B. Maller. The Macmillan Co.

\$2.75 $5\frac{1}{8} \times 7\frac{1}{2}$; xxiii + 559 New York

In this volume the authors pass from the statistical study of deceit to that of altruism and self-control. In all three cases they have found "evidence for doubting the efficacy of certain conventional efforts at character development in both secular and religious circles." Apparently they are somewhat surprised to find that in unselfishness, as in height or weight, the distribution is not bimodal.



STUDIES IN THE COMPARATIVE ABILITIES OF WHITES AND NEGROES. *Mental Measurement Monographs Serial No. 5.*

By Joseph Peterson and Lyle H. Lanier.

The Williams & Wilkins Co.
\$5.00 6×9 ; vi + 156 (paper) Baltimore

The outstanding result of our tests of adults is an enormous and reliable superiority of whites over negroes in all four group intelligence tests, this being true of the wholly non-verbal International rotator tests as well as of the Binet group, the Myers, and the Atkinson test. No sex differences in these tests are established.

In view of various sorts of evidence of effects of "cultural sets" on efficiency in different tests, effects which vary considerably from test to test, it is well to consider the question as to the degree of innateness of the racial differences here found an open one, though evidence points to a difference in native intellectual ability favoring the whites.



SOCIOLOGY AND SIN. *A Plea for the Exclusion of Uplift from Economics and the Political Sciences.*

By P. Sargant Florence.

W. W. Norton and Co., Inc.
\$1.00 $4\frac{1}{8} \times 6\frac{1}{2}$; 98 New York

The author wishes very strongly that sociology be pursued in the indicative, not the optative mood. It should concern itself with the careful and exhaustive study of things as they are and eschew the expression of how things ought to be. Then others, who should make it their specialty to envisage the ideals of society, can utilize the disinterestedly established truths for whatever ends they deem worthy.



THE HEALTH OF WORKERS IN DUSTY TRADES. II. *Exposure to Siliceous Dust (Granite Industry).* Public Health Bulletin No. 187.

By A. E. Russell, R. H. Britten, L. R. Thompson, J. J. Bloomfield (with sections on autopsy material by L. U. Gardner and on silica by A. Knopf).

U. S. Government Printing Office
\$1.15 Washington

$5\frac{1}{2} \times 9\frac{1}{8}$; iv + 206 (paper)

This bulletin, the second in an important series of investigations dealing with the health of individuals whose labors are in the so-called dusty trades, deals with a study of "silica dust of a definitely known composition in its effect on the health of the workers." Some of the salient points of this report are:

(a) The long period of service before the liability to tuberculosis becomes manifest (generally 20 years or more). (b) The sharp correlation between length of exposure to the dust and prevalence of tuberculosis and also the death rate from this disease. (c) The close relation between extent of dust exposure and health of the men. (d) The universal occurrence of silicosis among the workers. (e) The large proportion of workers finally succumbing to tuberculosis. (f) The almost invariably fatal form of the disease within a short time after the onset. (g) The different character of silicosis as manifested by X-rays compared with that shown where there is exposure to a dust with a much higher content of free silica. (h) The location of the tuberculous lesion, usually basal, where the disease complicates silicosis. (i) The absence of deaths from silicosis per se, tuberculosis ap-

parently always intervening. (j) The failure of workers to recover from their condition upon going into nondusty trades. (k) The high incidence of sickness of a severe nature from causes other than tuberculosis. (l) The rising sickness and mortality rates from tuberculosis due to longer use of the hand pneumatic tool. (m) The appallingly high death rates at the present time from tuberculosis, compared with normal industrial experience.

Many of the case histories are reported together with x-ray pictures of the chests of the individuals. A large number of tables and figures are included in the text. Unfortunately there is no index.



GENIALE MENSCHEN.

By Ernst Kretschmer.

Julius Springer

12 marks (paper)

Berlin

15 marks (cloth)

6 $\frac{3}{4}$ x 9 $\frac{1}{2}$; vii + 254

This volume is an interesting study of the personality (in the technical sense of modern constitutional research) of men of genius, and the biology and psychology of the origin and development of genius, by an outstanding and acknowledged leader in the field. The book is stated to be a revision and expansion of lectures dating from 1919 and in part separately published. The final section is a collection of portraits of distinguished men. It appears that the great philosophers have been mainly leptosomal in habitus. Pyknics are extremely rare among them. On the other hand pyknics are in the majority among the distinguished biologists of the past, including medical men as well as zoologists and botanists. There is no index, unfortunately.



THE CONQUEST OF THOUGHT BY INVENTION. *In the Mechanical State of the Future.*

By H. Stafford Hatfield.

W. W. Norton and Co., Inc.

\$1.00

4 $\frac{1}{2}$ x 6 $\frac{3}{4}$; 80

New York

The author, a successful inventor himself, apparently has considerable personal distaste for the automatism of life brought in by the machine, and its consequence, the suppression of individuality. But generally there is no opposition to this tendency. Most persons prefer security to the opportunity for self expression, and the whole tendency of physical, social, and political forces is in the direction of the State taking on the guidance of living. He looks toward the time when the white races

will settle down to live in a manner closely analogous to that of other routinized organisms such as ants and bees, and initiative will be withdrawn from society at large and most likely die out more or less rapidly. All this is happening, so it seems to me, in so inevitable a manner that any argument concerning its desirability appears futile.



MAN'S GREAT ADVENTURE. (*Thirty Stories of Mankind from the Dawn Man to the Man of To-day.*)

By Stephen Southwold.

Longmans, Green and Co.

\$1.75

5 $\frac{1}{2}$ x 7 $\frac{1}{2}$; 256

New York

This is an outline of history for boys of ten, written in the form of short stories attempting to typify the great human movements of the various periods from the Old Stone Age down to the present day. The aim of the author is to make his young readers realize, first, that the people of Rome, Greece, and Babylon were really human beings, and second, that Sherman spoke the truth about war. It is written that the good bishop Ulfilas, when he was translating the Scriptures into Gothic, left out the books of Kings because he feared the bad effect of so much fighting on his brother Goths. Now there is a good deal of the Goth in the average boy of ten; we fear that what will impress him in this book will be, not the suffering and cruelty of war, but the glamor of fighting.

FRANÇOIS RABELAIS. *Man of the Renaissance. A Spiritual Biography.*

By Samuel Putnam.

Jonathan Cape and Harrison Smith

\$3.50 $5\frac{1}{2} \times 8\frac{1}{2}$; xiii + 530 New York

Rabelais is one of the great legends of literary history. Read comparatively little, his name at least is known to all and Rabelaisian cults of one sort or another abound. He is known variously as a retailer of smutty stories (thanks to our Postoffice Department), a jolly wine-bibber, a devotee of the dissolute life and the belly, an irresponsible humorist, a great romancer. The author rescues his subject from the confusing enthusiasts and portrays him for what he primarily was, a great scholar, albeit humorous, literary, and coarse as befitted his time of the Renaissance. Mr. Putnam is one of America's greatest authorities on Rabelais and much learning goes into the book. But it is not pedantic and is never dull.



MAN'S PLACE AMONG THE MAMMALS.

By Frederic Wood Jones.

Longmans, Green and Co.

\$7.50 $5\frac{1}{2} \times 8\frac{1}{2}$; xi + 372 New York

Students of biological literature are already acquainted with the general thesis of this book: namely, that man must seek his ancestors not among the apes and monkeys but among the primitive *Tarsius*-like animals. A number of years ago the author first published his investigation on the origin of man. At that time his work received much adverse criticism. In this volume we have a restatement of the subject and one is inclined to think that the criticisms will be somewhat less severe, even if there are many who cannot follow the author all the way. In any event, at a time when the monkeys and apes are so much under fire there seems to be much of-

fered in these pages which cannot be ignored in a search for our fore-fathers.



MAN AND WOMAN. *A Study of Secondary and Tertiary Sexual Characters.*

By Havelock Ellis. Houghton Mifflin Co.

\$5.00 $5\frac{1}{2} \times 8\frac{1}{2}$; vii + 495 Boston

This edition is Ellis' well known book "remoulded and put into more popular form." The change involves some additions and some omissions from the earlier issues. In some ways we prefer the more original form, as represented for instance in the 6th edition previously noted in these columns.



GRUNDPROBLEME DER KONSTITUTIONSFORSCHUNG. *Würzburger Abhandlungen aus dem Gesamtgebiet der Medizin Band VI, Heft 3.*

By Hans Günther.

Curt Kabitzsch

2 marks $6\frac{5}{8} \times 9\frac{1}{2}$; 23 (paper) Leipzig

This *Antrittsvorlesung* delivered at the University of Leipzig is an interesting and valuable contribution to the literature of constitution studies. Its purpose is to examine critically the underlying concept of this branch of human biology. The need for such a philosophical examination of the case is well shown by the accompanying bibliography, in which every entry is accompanied by a quotation of the cited author's conception of what "constitution" means. It is plain that there is not yet any general agreement regarding fundamentals in this field.



THE WAY OF THE SEA. *The Corridors of Time VI.*

By Harold Peake and Herbert J. Fleure.

Yale University Press

\$2.00 $5\frac{1}{2} \times 8\frac{1}{2}$; viii + 168 New Haven

This volume of *The Corridors of Time* carries the story of man's early development through the period from 2100 to 1600 B.C. The authors conclude that the megalithic monuments do not date from remote prehistoric periods, but are the result of intercourse with the eastern Mediterranean not long before 2000 B.C.



TEMPERANCE OR PROHIBITION?

The Hearst Temperance Contest Committee, Francis J. Tietz, Editor

\$1.00 220 South St., New York

5 x 7½; xxii + 397

An epitome of the plans submitted in the contest conducted by the Hearst newspapers for a substitute for the present attempt at prohibition. The winning plan suggests the repeal of the Volstead act and the substitution for it of a law "defining the words 'intoxicating liquors' as 'all alcoholic products of distillation.'"



WOMEN IN GAINFUL OCCUPATIONS

1870 TO 1920. *A Study of the Trend of Recent Changes in the Numbers, Occupational Distribution, and Family Relationships of Women Reported in the Census as Following a Gainful Occupation. Census Monographs IX. By Joseph A. Hill.*

U. S. Government Printing Office

\$1.50 7 x 10; xvi + 416 Washington

This monograph deals not only with the general census tabulations for gainfully occupied women but also with a special study of the family relationships of gainfully occupied women in eleven selected cities. In view of the heated discussions of the wage-earning married woman that one often hears, it is interesting to note that only 9 per cent of the married women in the United States are wage-earners.

MAGIC SPADES. *The Romance of Archaeology.*

By R. V. D. Magoffin and Emily C. Davis.

Henry Holt and Co.

\$5.00 6 x 9½; xv + 348 New York

This book certainly succeeds in its intention of proving to the general reader that archaeology is a fascinating study. Professor Magoffin tells the story of modern discoveries in the Mediterranean region and Mesopotamia; Miss Davis deals with Britain, Scandinavia and America. Both show how interesting the reconstruction of a past era from its buried remains may be.



MEDICAL LEADERS from Hippocrates to Osler.

By Samuel W. Lambert and George M. Goodwin.

The Bobbs-Merrill Co.

\$5.00 5½ x 8½; viii + 331 Indianapolis

The non-medical reader will find in this book an excellent account of the history of medicine, correlated with the general intellectual development of the various periods. There is an abundance of picturesque detail in the narrative.



CAUSES AND PREVENTION OF NEONATAL MORTALITY. *United States Department of Labor. Children's Bureau.*

By Richard A. Bolt.

U. S. Government Printing Office

5 cents 5½ x 9½; 18 (paper) Washington

PREVENTION OF NEONATAL MORTALITY FROM THE OBSTETRICIAN'S POINT OF VIEW. *United States Department of Labor. Children's Bureau.*

By Fred L. Adair.

U. S. Government Printing Office

5 cents 5½ x 9½; 9 (paper) Washington

ANALYSIS AND TABULAR SUMMARY
RELATING TO JURISDICTION IN
CHILDREN'S CASES AND CASES OF
DOMESTIC RELATIONS IN THE
UNITED STATES. *U. S. Department of
Labor, Children's Bureau, Chart No. 17.*

By Freda Ring Lyman.

U. S. Government Printing Office

10 cents

Washington

9 x 11½; v + 33 (paper)



ZOOLOGY

INSECTS, TICKS, MITES AND VENOM-
OUS ANIMALS of Medical and Veterinary
Importance. Part I. Medical.

By Walter S. Patton and Alwen M. Evans.

Entomological Department, Liverpool

School of Tropical Medicine

20 shillings 7 x 9½; x + 786 Liverpool

This book replaces Patton and Cragg's *Textbook of Medical Entomology* which is now out of print. It forms the first of a series of four parts, each complete in itself. Although prepared primarily for the medical officer approaching the subject for the first time it will be of much use to the student of general and agricultural entomology, and invaluable to the medical officer in isolated tropical regions whose library is necessarily limited. Much space has been devoted to morphology and phylogeny, while very full notes are given on the early stages, bionomics and relation to disease of all the insects and Acari of medical importance. Included also is a great deal of more detailed information which at present is not available in entomological books or papers. The introductory section is followed by five sections devoted to the study of the external and internal anatomy of an arthropod, the Diptera being used largely as types. The remaining sections, twenty-two in all, are devoted to the systematic part of the course.

The book is beautifully illustrated with numerous photographs and drawings, mostly original. There is an excellent index but no list of references. A large sheet at the end of the book gives an illustrated key to the scheme of classification of the arthropods.



ANIMALS LOOKING AT YOU.

By Paul Eipper.

The Viking Press

\$3.00

6 x 9½; 163

New York

A fascinating book which will appeal to all animal lovers. The author, an almost daily frequenter of zoological gardens for 35 years, gives, in numerous brief sketches, some of his experiences with animals kept in captivity. In doing so, without attempting in any way to interpret the varied behavior of these animals, he succeeds in conveying to the reader a remarkably clear picture of the divergent personalities with which he was acquainted. He makes two pleas for animals kept in captivity—first, that there be sufficient space for each animal to permit of a reasonable amount of exercise, and, second, that there always be two of a kind kept together to relieve the dreadful fate of loneliness.

The song of the Orang, which gave him the most tremendous experience that he had ever had among animals, he describes as follows:

I had to wait for hours, but at last as the darkness set in, and shortly before Goliath retired to his sleeping chamber, it came to pass. Aw—Aw—Aw, soft and dull but very quick, like the pulsing of a motor. For ten seconds it came beating without pause from his throat, and was then broken by a sighing, sobbing intake of breath, and then swelled out again, this time an octave higher, and in a strong crescendo. Again a sigh and the Aw—Aw—Aw burst forth again, on a higher note than ever. The cry beat painfully against my ear-drums, and I saw how swollen was the Orang's throat pouch; and now mingled with the singing came a thunderous nerve-racking long-drawn-out H—u—u—u—

u-h. The mighty song resounded in powerful alternations, Aw—Aw—Aw—H—u—u—uh, as tremendous as the lions' roar. It was the song of primitive life, the thunderous speech of nature.

He tells of two giraffes tamed by a hunter and led hundreds of miles through African wilderness and over a high mountain range; of the white mouse and the venomous snake who dwelt amicably together although other mice were instantly devoured when put in the cage with the snake; of days spent with a group of orang-outangs—44 in number—in an acclimatization camp in southern France and of a trip from this camp to Berlin accompanied by a four year old gorilla and a young chimpanzee.

The book is illustrated with a group of very fine photographs, the most appealing perhaps being those of the oranges.



A NEW RODENT FROM THE GALAPAGOS ISLANDS. *Publication 261.*

By Wilfred H. Osgood.

Field Museum of Natural History
75 cents $6\frac{1}{2} \times 9\frac{1}{2}$; 4 (paper) *Chicago*

This makes the fourth or fifth rodent found on the islands, the first having been discovered by Charles Darwin, during his famous visit. It is called *Nesoryzomys darwini*. "With the addition of *N. darwini* to the other forms above mentioned, the rodents of the islands take on considerably more importance than formerly and will doubtless need serious consideration in speculation regarding the derivation of the insular fauna."



ANNOTATED BIBLIOGRAPHY OF THE MOSS MITES (*Oribatoidea*, *Acarina*).

By Arthur Paul Jacot.

Catholic Mission Press
50 cents $5\frac{1}{2} \times 8\frac{1}{2}$; 60 (paper) *Tsingtao*.

This annotated bibliography of the moss

mites, chronologically arranged, is in three sections. In the first part the author places all the contributions which embody original material, these being grouped as follows: Eighteenth century; Early writers (to 1875); Italian and English era (1876–1894); American and Dutch era (1895–1904); Italian recrudescence (1905–1912); English recrudescence (1913–1919); German recrudescence (1920–). The other two sections of the bibliography contain miscellaneous comparative references, and compendiums, texts, translations and relists.



HALIOTIS. *Liverpool Marine Biology Committee Memoirs on Typical British Marine Plants and Animals.* XXIX.

By Doris R. Crofts.

The University Press of Liverpool
10 s. 6 d. *Liverpool*

6 x $9\frac{1}{2}$; viii + 174 + 8 plates (paper)

Aside from its interest biologically, *Haliotis* is of considerable economic importance, the shells being widely used in ornamentation, while there are several edible forms which form the basis of a thriving industry in California and Japan. The author of this book has brought together widely scattered material on the group of molluscs to which *Haliotis* belongs, many doubtful points have been cleared up, and much new material is contributed in the field of bionomics, cytology and physiology. Included in the work are 31 text-figures and 39 plates. There is a literature list of 69 titles.



A HANDBOOK OF THE MOSQUITOES OF NORTH AMERICA. *Their Structure, How They Live, How They Carry Disease, How They May be Studied, How They May Be Controlled, How They May Be Identified.*

By Robert Matheson. Charles C. Thomas
\$5.50 6 x 9; xvii + 268 Springfield, Ill.
A simple, clear succinct account.



GENERAL CATALOGUE OF THE
HEMIPTERA. Fascicle II. Mesoveliidae.
By Géza Horváth. Smith College
50 cents Northampton, Mass.

6 x 9; 15 (paper)

GENERAL CATALOGUE OF THE
HEMIPTERA. Fascicle III. Pyrrhocoridae.
By Roland F. Hussey, with Bibliography by
Elizabeth Sherman. Smith College
\$1.50 Northampton, Mass.

6½ x 9; 144 (paper)



KEY-CATALOGUE OF PARASITES RE-
PORTED FOR PRIMATES (MONKEYS
AND LEMURS) WITH THEIR POS-
SIBLE PUBLIC HEALTH IMPORTANCE
by C. W. Stiles and Albert Hassall, and KEY-
CATALOGUE OF PRIMATES FOR
WHICH PARASITES ARE REPORTED.
by C. W. Stiles and Mabelle Orleman Nolan.
United States Treasury Department, Public
Health Service, Hygienic Laboratory Bulletin
No. 152.

U. S. Government Printing Office
35 cents Washington

5½ x 9½; iv + 192 (paper)



MORPHOLOGY AND DIVISION OF
CHLAMYDOMONAS with Reference to the
Phylogeny of the Flagellate Neuromotor Sys-
tem. University of California Publications
in Zoology, Vol. 33, No. 7.
By J. McA. Kater.

University of California Press
60 cents Berkeley

7 x 10½; 44 + 6 plates (paper)

BOTANY

MANGROVE FORESTS OF THE MA- LAY PENINSULA.

Malayan Forest Records No. 6.

By J. G. Watson.

Federated Malay States Government
Conservator of Forests, Kuala Lumpur
\$3.00 or 7 shillings post free

The mangrove forests or swamps of the
Malay Peninsula cover an area of about
430 square miles. Of this area over 400
square miles have been constituted forest
reserves. The principal species in these
forests belong to four families, the Rhizo-
phoraceae, Lythraceae, Verbenaceae, and
Meliaceae. Subsidiary species fall in 15
families. The present volume is a de-
tailed account of the general ecology of
these forests, using the term "ecology" in
the widest sense. It is extensively and
beautifully illustrated with photographs,
and will be of quite as great interest to
the general botanist as to the student of
forestry, for whom it was primarily writ-
ten. It contains a bibliography of 55
titles and a detailed index.



STEPHEN HALES, D.D., F.R.S. *An
Eighteenth Century Biography.*
By A. E. Clark-Kennedy.

The Macmillan Co.
\$6.00 5½ x 8½; xii + 256 New York

In these days, when many of the clergy
are actively hostile to science and the rest
are more interested in reconciling it with
theology than in understanding it, a
clergyman who spent his spare time in
scientific work would be looked on with
astonishment and even, perhaps, with a
certain disapprobation. In the eighteenth
century men thought differently. There
is no evidence that anyone felt that "the
good Pastor Stephen Hales" sullied his
cloth by his experiments on vegetable

statics, although Pope was squeamish over his vivisections. Those who wish to learn more about the work of a remarkable man will do well to read this book.



COAL MEASURE PLANTS.

By R. Crookall. Longmans, Green and Co.
\$5.00 5½ x 9; 80 + 39 plates New York
12 s. 6 d. Edward Arnold and Co.
London

This book deals with the external morphology of 240 of the more common and characteristic plants of the British Coal Measure. Brief descriptive notes are given in terminology easily comprehended by the amateur naturalist, but the author has in no sense made a popular field guide. Students of botany, geology and mining will find it an excellent introduction to paleobotany. The work includes numerous diagrams and line drawings and a group of excellent plates, also a list of species occurring in the book and an index.



OUR MOST POPULAR TREES.

By Lydia Northrop Gilbert.
George Sully and Co., Inc.
\$1.50 4 x 6½; 110 New York

A pocket guide for nature lovers, students and artists. It contains forty-eight full page illustrations in color, showing in detail the tree, bark, fruit, blossom and leaf.



LES LILIIFLORES DU QUÉBEC. (*Liliacées, Pontédériacées, Iridacées, Joncacées.*) Contributions du Laboratoire de Botanique de l'Université de Montréal—No. 14.

By Frère Marie-Victorin.

Laboratory of Botany, University of Montreal
\$1.50 6 x 9; 202 (paper) Montreal
ADDITIONS AUX CYPÉRACEES DE L'AMÉRIQUE DU NORD. Contributions

du Laboratoire de Botanique de l'Université de Montréal—No. 15.

By Frère Marie-Victorin.

Laboratory of Botany, University of Montreal
50 cents 6 x 9; 16 (paper) Montreal



VOCABULARY OF PLANT SOCIOLOGY.

By J. Braun-Blanquet and J. Pavillard.
Translated by F. R. Bharucha.

F. R. Bharucha
1 shilling Botany School, Cambridge
6½ x 9½; 23 (paper)



MORPHOLOGY

THE CHROMOSOMES IN MAN: SEX AND SOMATIC. *Memoirs of the University of California, Volume 9, No. 1.*

By Herbert M. Evans and Olive Swezy.

University of California Press
\$1.50 Berkeley

10 x 13; 41 + 11 plates (paper)

This short monograph summarizes briefly what has been done to date to elucidate the chromosomal organization in the cells of man. Most of it is occupied with a description of the original work of the authors. This is divided into investigations of the sex and somatic cells. For the former, there were utilized freshly preserved testicular material from six males, and for the latter sections from two embryos, from the uterus of a fifteen year negress, and from a carcinoma of the lip in a fifty-five year man. Definitive observations are recorded on the number of chromosomes, the differentiation into autosomes and X-Y chromosomes, the kinetics of the chromosomes during mitosis, and the mensuration of chromosomes. There are a considerable number of plates, reproducing chromosomal figures in large magnification.

TEXT-BOOK OF EMBRYOLOGY.

By F. R. Bailey and A. M. Miller.

William Wood and Co.

\$7.00 6½ x 9½; xvi + 687 New York

A fifth edition. While the general plan of the original text has been adhered to there has been much revision, particularly in the chapter on the nervous system. Parts of the book have been rewritten where recent investigations have modified the views expressed in the earlier editions. New figures have to some extent replaced old figures and new illustrations have been added.



THE ESSENTIALS OF HUMAN EMBRYOLOGY.

By Gideon S. Dodds.

John Wiley and Sons, Inc.

\$4.00 5¾ x 9; vii + 316 New York

A textbook for medical and pre-medical students. Recognizing that there are many subjects besides embryology which the student must master, the author has tried to make his book as brief as is consistent with an adequate treatment. It is clearly and interestingly written and well illustrated and indexed.

PHYSIOLOGY AND
PATHOLOGY

NOUVEAU TRAITÉ DE MÉDECINE.

Fascicule XVI. *Pathologie du foie et des voies biliaires.*

Chapters by various authors. Masson et Cie

125 francs 6¾ x 9½; viii + 1048 Paris

This volume represents a tremendous amount of work on the part of the several contributors. It is interestingly written and well illustrated, but it is very poorly bound. It is written largely from the

point of view of the pathologist and the classifier of disease. The American reader today, who is perhaps more interested in trying to detect disturbances in liver function before the patient is bloated and hopelessly ill, will be somewhat disappointed because, so far as we can find, there is little or nothing about the practical use of the dye tests which are now so commonly employed. Similarly, there appears to be nothing about the icterus index or the van den Berg test, which has proved so helpful in the differentiation of the various types of jaundice. It is possible that these topics are discussed somewhere in the book, but if the reviewer missed them he does not feel as culpable as he would if there had been an index to help him in his search. The lack of interest in the physiologic aspects of liver disease is shown also by the absence of any reference to the work of Mann and his students, work which has thrown so much light on the functions of the liver.

It comes somewhat as a shock to see that the field of medicine has now become so enormous that it is possible to write a thousand pages on the diseases of one organ of the body. What is still more disturbing is the fact that these one thousand pages were not sufficient for the proper handling of the subject, and that many chapters have been left sketchy and inadequate, so far as the specialist is concerned. Much of the inadequacy must, of course, be ascribed to the fact that no one yet knows enough about the subject of liver function and liver disease, but some of it is due to the fact that no one man in any one part of the world can keep quite up to date, especially during the year or more in which he is swamped with the actual labor of writing a book.

And so we feel that any disappointment which a reviewer may feel at not finding

what he wants here and there, should not blind him to the fact that an enormous amount of useful information has been gathered in one place, and that the men who did the work deserve praise and many thanks from those whom they have served. And even if they have quarried mainly from the works of their own countrymen to the neglect of the writings of foreigners, let us take advantage of this human failing. Let Germans and Englishmen write similar texts in the same way and then we in America, by consulting three books on any one subject, can gain access to most of what is known in Europe on this subject. It may not be a bad thing for a student in America to learn that the discovery which he has always credited to Mann is ascribed by a French textbook writer, who never heard of Mann, to a Frenchman whom the American never heard of.



THE IMMUNOLOGY OF PARASITIC INFECTIONS.

By William H. Taliaferro.

The Century Co.

\$6.00 5½ x 8½; xv + 414 New York

No better idea of the *raison d'être* of this important book can be given than by quoting from the preface where the author says:

The present volume is not, in any sense, intended to be a treatise on immunology, but a compilation, and as far as possible, an evaluation of the mass of immunological work that has been done on infections with animal parasites. Besides stimulating interest in this field, I hope that the present work will hasten the incorporation of these experimental data into both parasitology and immunology, where, in spite of a growing interest during the past few years, it has been largely neglected. By achieving this, the parasitologist will undoubtedly gain new concepts for many of his experimental studies on infections, and the immunologist can obtain unique material for certain immunological questions.

The book has been especially arranged from the point of usefulness to student and investigator. Much pains has been taken to avoid confusion in nomenclature. The value of the book for reference purposes has been greatly enhanced by the lengthy literature list, the catalogue of parasites considered in the text and author and subject indices.



DIET AND EFFICIENCY. *A Five-Year Controlled Experiment on Man.*

By Harold H. G. Holck.

University of Chicago Press

\$1.00 5½ x 9; viii + 72 (paper) Chicago

In the long and honorable list of men who have martyred themselves to the cause of scientific progress, the author of this little work certainly has a conspicuous place. For a total of about 525 days he subjected himself to the practice of *Fletcherizing*, i.e., thorough to excessive mastication of food taken only when actually hungry and stopped as soon as satisfied. What Brillat-Savarin or the more modern exponents of the art of the *gourmet* would say of such habits we shudder to think, but please remember Fletcher advocated his system for health, not happiness, which is another thing. A number of biochemical and physiological observations were made daily during the course of the experiment, and compared with the results of a normal control period. The conclusions of these extended investigations are that Fletcherizing decreased muscular endurance, typewriting accuracy and basal metabolism, had no significant effect on blood pressure, pulse, oral temperature, sleeping time, mental multiplication, and typewriting speed, improved efficiency in solving chess problems and the approach in body weight toward common standards.

LES ANOMALIES DU COMPLEXE VENTRICULAIRE ÉLECTRIQUE *Leur Importance en Clinique. (Essai d'Électro-Cardio-Pronostic.)*

By J. Robert Lévy.

Masson et Cie

30 francs 6½ x 10; 202 (paper) Paris

Perhaps the greatest need of the cardiologist today is for more knowledge in regard to prognosis. Since the time of Imhotep the patient with heart disease has always been concerned most about his future: Is he going to drop dead? Must he hurry about making his will? Must he live as a valetudinarian, or can he drive at his business and at his golf ball as usual? Since these questions must be answered somehow it is a pleasure to find a book in which the prognosis of heart disease is based on the actual experience of the author, a man who has taken the trouble to follow up many of his patients to see how long they survived the discovery of their disease. Too many books are written by men who either haven't enough experience or who haven't the sense to rely on it. They haven't the vision to see that it is much more important and profitable to put down clearly that which they have seen and learned in the clinic and the laboratory than to rehash that which they have read in books. Although Dr. Levy writes largely from his own experience he refers also to over 400 articles written by other men working in all parts of the civilized world.



HOOKWORM DISEASE. *Its Distribution, Biology, Epidemiology, Pathology, Diagnosis, Treatment and Control.*

By Asa C. Chandler.

The Macmillan Co.

\$5.00 6½ x 9½; xii + 494 New York

A comprehensive treatise which will be invaluable as a general reference book to members of the medical profession as well as investigators. The author has brought

together all of the important results which recent researches have revealed and has given to his readers much material which hitherto has not been easily attainable. The book contains a separate section devoted to "Technical Methods," a lengthy bibliography and an index.



PHYSIOPATHOLOGIE ET TRAITEMENT DU DIABÈTE SUCRÉ.

By H. Chabanier, M. Lebert and C. Lobo-Onell.

Masson et Cie

50 francs 6½ x 10; 441 (paper) Paris

This book must be of considerable interest to students of diabetes because it contains so full a discussion of the threshold in kidney function which determines the point at which sugar accumulating in the blood flows over into the urine. We know of no other place in which the subject is so fully treated. Much research work is reported: work designed to show how the glycosuric threshold is influenced by the degree of glycemia, by the giving of insulin, and by other factors. The authors discuss also what they believe to be the basal defect in diabetes and the ways in which insulin affects this. This part of the book is not so valuable, however, because it is not up to date and does not appear to add much to the stock of knowledge on this point. The first half of the book is taken up with a discussion of the physiology of the disease and the second with problems of practical treatment. There are many references to the literature and there is a fair index.



TRAITÉ DE PHYSIOLOGIE NORMALE ET PATHOLOGIQUE. Tome VIII. *Physiologie Musculaire Chaleur Animale.*

By Léon Binet, G. Bourguignon, P. Chailley-

Bert, J. Gautrelet, L. Lapicue, J. Lefevre, R. Leriche, A. Policard, A. Strobl, G. Weiss.

95 francs (paper) *Masson et Cie*
110 francs (bound) $6\frac{5}{8} \times 9\frac{1}{2}$; 742 *Paris*

Another volume in a comprehensive series on human physiology which has been previously noted in these columns. Contrary to the promise of the title, the portion devoted to pathological states is minimal; the references are meager and scattered, and the book has no general index. It does not compare favorably with the German series issued under the editorship of Bethe.



LE CŒUR. *Les Médicaments Cardiaques et l'Électrocardiogramme. Recherches Expérimentales du Laboratoire de Thérapeutique de l'Université de Liège.*

By F. Henrijean. *Masson et Cie*
50 francs *Paris*

$6\frac{1}{4} \times 10$; xxiv + 416 (paper)

The researches with which this volume deals were begun on the pharmacological problem of the mechanism of the action of drugs on the heart, a question which led to the more general problem of the nature of the heart action. The author concludes that the origin of the cardiac contractions is in neither the heart muscle nor the nerves, but in tissues which preserve the mixed character of the embryonic heart tissue, being both contractile and conductive.



NOUVEAU TRAITÉ DE MÉDECINE.

Fascicule V (Tome II). Le Cancer.

By Gustave Roussy with the collaboration of Roger Leroux and Maurice Wolf.

Masson et Cie
100 francs *Paris*

$6\frac{1}{4} \times 9\frac{3}{4}$; viii + 846

This is a revised edition, completely re-

written and considerably enlarged, of Dr. Roussy's cancer volume published in 1922 as a part of the *Nouveau Traité de Médecine*. In its present form it is one of the best general accounts of cancer available. Every aspect of the subject is discussed. The range and thoroughness of the work may be indicated by the statement that the bibliography, which includes only writings consulted or cited in the text, covers 69 closely printed, double column pages of small type. The volume is extensively and well illustrated, and altogether constitutes a reference work of first class importance and usefulness.



LE LIQUIDE CÉPHALO-RACHIDIEN. *Physiologie et Exploration du Système Ventriculo-Méningé.*

By Dr. Riser. *Masson et Cie*
28 francs $6\frac{1}{4} \times 9\frac{1}{8}$; 250 (paper) *Paris*

The primary purpose of this interesting and useful volume is to give a well-rounded account of the important researches on the physiology of the cerebrospinal fluid which have been carried out in the *École Neurologique* at Toulouse during the last decade under the direction of Professor Cestan. The author formally disclaims any intention of making a systematic general review of knowledge regarding the cerebrospinal fluid. Instead it is especially devoted to a critical exposition of the various recent methods of exploration by the injection of air, colored solutions, lipiodol, etc., and their medico-surgical applications.



THE ESSENTIALS OF CHEMICAL PHYSIOLOGY *for the Use of Students.*

By W. D. Halliburton, J. A. Hewitt and W. Robson. *Longmans, Green and Co.*

\$3.00 $5\frac{1}{2} \times 8\frac{1}{2}$; xii + 383 *New York*

The author of this well known text book has been assisted in the preparation of this, the twelfth, edition by two collaborators. The general scheme of the book is unchanged but there has been a rearrangement of the detailed material and the necessary additions made to bring the book up to date.



LE MÉTABOLISME BASAL.

By Marcel Labbé and H. Stévenin.

Masson et Cie

40 francs 6½ x 9½; 343 (paper) Paris

The authors have prepared a good systematic treatise on basal metabolism, one which will doubtless be of great assistance to the young Frenchman who takes up the study of the subject. It is doubtful if it will be of much interest to the American specialist except at such times as he is looking for references to the work of French investigators. As anyone can see by glancing at the names of the authors quoted throughout the book, Labbé and Stévenin had to depend on Americans for most of their information in regard to the clinical application of calorimetry.



PELADES ET ALOPÉCIES EN AIRES.

Les Syndromes Alopeciques V.

By R. Sabouraud.

Masson et Cie

80 francs 6½ x 10; 378 (paper) Paris

This, the last of the five monographs on diseases of the scalp to which the author has given thirty years of research, is a model of thoroughness. Dr. Sabouraud emphasizes as etiological factors, congenital syphilis, tuberculosis, and disturbances of the endocrine glands and sympathetic system. There is a bibliography of 27 pages but no index.

LABORATORY OUTLINES IN COMPARATIVE PHYSIOLOGY.

By Charles G. Rogers.

McGraw-Hill Book Co., Inc.

\$1.50 5½ x 9; vii + 130 New York



ECONOMIC BENEFITS OF ERADICATING TUBERCULOSIS FROM LIVESTOCK. U. S. Department of Agriculture Miscellaneous Publication No. 66.

By John R. Mohler, A. E. Wight, and L. B. Ernest. U. S. Government Printing Office

5 cents 5½ x 9½; 24 (paper) Washington



BIOCHEMISTRY

A CHEMICAL DICTIONARY. *Containing the Words Generally Used in Chemistry, and Many of the Terms Used in the Related Sciences of Physics, Astrophysics, Mineralogy, Pharmacy, and Biology, with Their Pronunciations. Based on Recent Chemical Literature.*

By Ingo W. D. Hackh.

P. Blakiston's Son and Co., Inc.

\$10.00 6½ x 9½; viii + 790 Philadelphia

A highly useful book. The author has, with great diligence and skill, compiled a dictionary which remarkably well fulfills the requirements that such a book demands. Besides describing in simple modern terms all the terminology, theories, laws, methods, apparatus, etc., which have to do directly with chemistry, he includes the vocabulary of allied sciences and industries, and the names of investigators who have contributed to the development of chemistry. Tables, diagrams and numerous other illustrations add greatly to the value of the book.

PRAKTIKUM DER PHYSIOLOGISCHEN CHEMIE. *Zweiter Teil, Blut-Harn.*
By P. Rona and H. Kleinmann.

Julius Springer
Berlin

39.60 marks

$5\frac{1}{2} \times 8\frac{1}{4}$; xix + 764 (paper)

This laboratory manual of the physiological chemistry of the blood and urine maintains the high standard set in the earlier parts. The present volume, which completes the work, closes with a chapter on the mathematical theory of errors, least squares, etc., by Dr. G. Ettisch. Dr. Rona, in the preface, says that he hopes that this chapter will sharpen the wits of the worker relative to the significance of the numerical results of chemical analyses. There is a detailed index.



HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 303.* Containing the following articles: *Methoden der Viscosimetrie kolloider Lösungen*, by Rudolf Köhler; *Methoden zur Bestimmung des kolloid-osmotischen Druckes in biologischen Flüssigkeiten*, by Marie Wreschner; *Methoden zur Bestimmung der elektrischen Struktur kolloider Stoffe, insbesondere der Biokolloide*, by Reinold Fürth.

9 marks

Urban und Schwarzenberg
 7×10 ; xx + 154 (paper) Berlin

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 305.* Containing following articles: *Methodik der mitogenetischen Strahlenforschung*, by Alexander Gurwitsch; *Die Mikroveraschung*, by K. O. Henckel; *Schonendes Eindampfen bei niederen Temperaturen*, by Ernst Jantzen and Hans Schmalfluss; *Die Capillaroskopie mit starken Vergrößerungen*, by Paul Vonwiller and Alfred Vannotti; and *Der isoelektrische*

Punkt von Protoplasten und seine Ermittlung, by Hans Pfeiffer.

Urban und Schwarzenberg

11 marks 7×10 ; 194 (paper) Berlin

Two further additions to this valuable handbook series. The first will be of great interest to the physical chemist, the latter to the experimental biologist.



A CRITICAL AND HISTORICAL STUDY OF THE PECTIC SUBSTANCES OF PLANTS. *Department of Scientific and Industrial Research, Food Investigation Special Report No. 33.*

By M. H. Branfoot.

H. M. Stationery Office

3s. 6d. net $6 \times 9\frac{5}{8}$; x + 154 (paper) London

This monograph deals with the chemistry of the pectic compounds, as well as their functions in the plant economy and the action of fungi and bacteria on them. The results are of value in the storage of fruits, the making of fruit jellies, and the retting of flax. There are an index of authors and a bibliography.



SEX

LAWS CONCERNING BIRTH CONTROL IN THE UNITED STATES.

Committee on Federal Legislation for Birth Control

25 cents $5\frac{3}{8} \times 8$; 39 (paper) New York

This is a useful pamphlet to preserve for reference. It quotes the laws relative to birth control in each state having them. Curiously enough, there is only one state in the Union, Mississippi, which clearly prohibits a physician from giving information on the subject to his patients. Connecticut alone prohibits the use of contra-

ception. The laws of 26 states do not mention the prevention of conception.



WHAT IS RIGHT WITH MARRIAGE.

An Outline of Domestic Theory.

By Robert C. Binkley and Frances W. Binkley.

D. Appleton and Co.

\$2.50 5½ x 8; xii + 262 New York

Unlike most present-day books on marriage, this is a Credo rather than a case study. The authors, a young married couple trained in the social sciences, obtain their "outline of domestic theory" in large part deductively from postulates as to the nature of the family. They conclude that, while the family has been stripped of many of its former functions by other agencies, it still serves the "affectional" function and the consequent enhancement of personality. As to sex monopoly they conclude "that the ideal is good as a plan of life, but bad as an enforced element of the marriage institution."



BIOMETRY

THE DEVELOPMENT AND GROWTH OF THE EXTERNAL DIMENSIONS OF THE HUMAN BODY IN THE FETAL PERIOD.

By Richard E. Scammon and Leroy A. Calkins.

University of Minnesota Press

\$10.00 8½ x 11½; xxiii + 367 Minneapolis

The present publication is a report on a part of a systematic quantitative study of the growth and structure of the body during the fetal period. It consists of an account of the changes in the dimensions and external proportions of the body as determined from a large number of original observations and from a colligation of all available published data of other investigators. These data have been treated analytically, studied for the effects of various important arti-

facts upon them, and are presented in condensed tabular, graphic, and analytic forms. As a whole, the investigation has been directed to the study of the trends of central tendency of the various dimensions, although certain observations regarding their variability are included.

The most important conclusion reached is that concerning the interrelationships of the various external dimensions of the body in the fetal period. It is stated by the authors as follows:

First, the growth of the external dimensions of the body in the fetal period is directly proportional to the linear growth of the body as a whole and that of other external dimensions of the body.

Second, the absolute growth rate of each external dimension of the body, with respect to the absolute linear growth rate of the body as a whole, is usually established when the fetus is between 3 and 10 cm. in crown-heel length, and remains unchanged to birth.

The whole monograph is done with meticulous care of detail, and sound biometric reasoning applied to the general analysis. There is a complete bibliography alphabetically arranged and summaries of original data and biometric constants but unfortunately no general index. It will stand for some time as the definitive work in its field.



PHYSICAL MEASURES OF GROWTH AND NUTRITION. *School Health Research Monographs Number II.*

By Raymond Franzen.

American Child Health Assoc.

\$1.00 (paper)

New York

\$1.25 (cloth) 6½ x 9½; xii + 138

This investigation was based on measurements of about 7500 public school children of the fifth and sixth grades in seventy schools scattered over 38 states. Its main object was to obtain a testing method to be used in the development of school health programs. The children

were of both sexes, white, American born, of 10, 11 and 12 years. The analysis of the anthropometrical measurements yields much interesting and valuable data in the general field of growth, development and nutrition. Much of this is presented in tabular form. At the end of chapter III is a summary of the measures which were found to yield satisfactory results in obtaining an approximation to the nutritional status of the individual. They are as follows:

Actual weight minus the weight to be expected from height. Actual weight minus the weight to be expected from height, bisacromial width, chest dimensions, and width of hips. Actual upper arm girth minus the upper arm girth to be expected from height, chest dimensions, and width of hips. Actual calf girth minus the calf girth to be expected from height, chest dimensions, and width of hips. Actual amount of subcutaneous tissue over the biceps minus the amount of subcutaneous tissue over the biceps to be expected from height, chest dimensions, width of hips, and bisacromial width.

Appendices at the end of the report give: (a) Technique followed in obtaining physical measurements, (b) Basic data, (c) Statistical technique, and (d) Supplementary data.



PSYCHOLOGY AND BEHAVIOR

MASTER OF MY FATE. *A Discussion of Personality and Behavior with Emphasis upon Self-Direction.*

By Herschel T. Manuel. The Century Co.
\$3.00 5½ x 7½; xii + 329 New York

This book is so good, so terribly good, indeed so perfectly priceless, that we must confess at the start that justice cannot possibly be done to it in the limited space we can spare. Up to the present the production of those fundamentally important and valuable elements of our native fauna, the 100 per cent American, the Ro-

tarian, and Mr. Babbitt, has been left mainly to chance and the operation of un-directed natural forces. Human biology is a young science, and has not yet, up to now, done much in the way of the constructive development of a scientific technique for the mass production of a standardized, sound citizenry. Now we have a pioneer treatise, which *may*, of course, possibly be improved upon with the passage of time, but we doubt it. The author is Professor of Educational Psychology at the University of Texas. The book is obviously written *con amore*, and we recommend it with completely equal lack of reservation to all those who want to become Babbitts and to all those who don't, which makes it almost unanimous.

The book is divided into three parts. The first deals with biological and psychological foundations of human behavior. The treatment of these matters is along sound lines, but in no way so extraordinary as to warrant writing home about it. The second and major part of the book is where the really constructive and forward-looking contribution finds its home. It has to do with the development of personality and behavior along right lines. It includes chapters on such basic matters as appearance, manners, the quest of culture, character and morals, etc. A few of the section heads in this part of the book will indicate how thorough, and how right, it all is. We start with "Another reason for a bath," and go on to good advice about "Soap, water and perfume." Then come concise but adequate instructions about how to shake hands. A short, but how useful section, suggests that "Unpleasant sounds will not make friends," and points out that smacking the lips, drawing air through the teeth, noisy sipping of tea, and various other such sounds are to be avoided in building personality.

(Reginald the Office Boy says that, in the interest of that systematic thoroughness which has been instilled into him as an ideal, he thinks the Professor might well have made his list of unpleasant sounds even more inclusive than he did.)

To continue: What could be more helpful than the advice to "Stand tall and sit straight." A section of "Retouching better than masking" gives the girls superb instruction in the art of really effective make-up. Dress is thoroughly gone into; "Dress is more than drapery," "Line and form a first consideration," "Consider the silhouette," are sample sections. Then follows a priceless chapter on the general principles of effective action. We should like to quote from it, but space is lacking. There follows a chapter on language and speech, in which sections are devoted to such matters as: "Penmanship should be legible," "The voice can be improved," "The dictionary might help," "Avoid a lazy jaw," "Effective speech requires thinking." The next chapter tells of "Self and the other fellow," which instructs in "friendliness. This leads naturally to "Manners in making men." Here Emily Post (whose great treatise is appropriately included in the bibliography) finds a rival, and a dangerous one. What could be more perfect than this section headed "Chew your gum in private," which we must quote in full:

Unnecessary practices should be avoided where they are likely to annoy others. The chewing of gum, the eating of candy and the use of tobacco are frequent transgressions of this principle. Nor can one justify the lack of privacy too frequently shown in powdering the nose, manicuring the nails and combing the hair. It is not universally entertaining to have thrust before one the monotonous grind of a lower jaw, the nervous sucking at a cigarette or the dab-dab-dab of an attempt to restore a vanishing complexion.

Detailed instructions are given about introducing people to each other, how to behave at the table—no "thoughtful

reader," to whom the publisher's blurb recommends the book, need ever again be embarrassed about toothpicks, forks, soup, etc.—getting up a dance, and so on, and so on. Paragraph No. 15 of the table instructions contains the following sentence, which illustrates the soundness and candor of the whole: "Alcoholic drinks or other harmful articles should be courteously declined."

Here we must regretfully leave Part II. There is a lot more of it, but if what we have already called attention to does not make the reader of this review dash out and buy the book at once, our hand has wholly lost its cunning.

Part III presents a program of self-direction, and is largely composed of a "rating scale." This "rating scale" contains 502 separate items. You are instructed to rate yourself 0, 1, or 2 relative to each of these items. The meaning is that 0 is the least desirable rating, 2, the most desirable rating, and 1 average. By the use of this scale according to directions "the ambitious individual may analyze his difficulties and initiate efforts toward improvement."

We can bring to a close this all too brief notice of a great book in no more fitting manner than by quoting that sublime thought of Samuel Butler:

Oh God! Oh Montreal!



BRAIN MECHANISMS AND INTELLIGENCE: *A Quantitative Study of Injuries to the Brain.*

By K. S. Lashley.

The University of Chicago Press

\$3.00

Chicago

6 x 9; xiv + 186 + 11 plates

The investigation herein reported is part of a general program on the analysis of the neural mechanisms which play a part in learning. Dr. Lashley has done a re-

markably fine piece of work, and his results are of the utmost importance in the field of neurological investigation. He has adequately summarized his study on the last two pages of his book. Unfortunately space will permit in this review only the inclusion of the inferences which he draws from his experiments:

The learning process and the retention of habits are not dependent upon any finely localized structural changes within the cerebral cortex. The results are incompatible with theories of learning by changes in synaptic structure, or with any theories which assume that particular neural integrations are dependent upon definite anatomical paths specialized for them. Integration cannot be expressed in terms of connections between specific neurons.

The contribution of the different parts of a specialized area or of the whole cortex, in the case of non-localized functions, is qualitatively the same. There is not a summation of diverse functions, but a non-specialized dynamic function of the tissue as a whole.

Analysis of the maze habit indicates that its formation involves processes which are characteristic of intelligent behavior. Hence the results for the rat are generalized for cerebral function in intelligence. Data on dementia in man are suggestive of conditions similar to those found after cerebral injury in the rat.

The mechanisms of integration are to be sought in the dynamic relations among the parts of the nervous system rather than in details of structural differentiation. Suggestions toward a theory of the nature of these forces are presented.

The author devotes a chapter to the comparison of his experiments on rats with experiments on the dog, the monkey, and man. The book is illustrated with numerous figures showing the brain lesions of the animals under experimentation, and with tables exhibiting the performance of these animals.

There is a bibliography of 137 titles, and an index.



EXPERIMENTAL STUDIES OF ADAPTIVE BEHAVIOR IN CATS. *Comparative Psychology Monographs, Vol. 6, No. 1.*

By Donald K. Adams.

The Johns Hopkins Press

\$2.50 7 x 10½; 168 (paper) *Baltimore*

The author comes out strongly against the description of psychology in terms of the conditioned reflex of the behaviorist. He maintained a colony of cats in the Yale Institute of Psychology for three years, and performed experiments upon them in three of the Thorndike puzzle boxes. "In each case the presence of what Hobhouse calls practical ideas is inferred. The presence of articulate ideas is inferred from the behavior of Pete in box A, from that of Trey in Box B1 and from that of Fitz in Box C and is suggested by other behavior." He reaches a theory that agrees with that stated by Tolman in 1928, a summary of which is quoted in the text.



GROWTH IN RELIGION. *An Introduction to Psychology for Teachers of Religion.*

By Harold J. Sheridan. *Cokesbury Press*

\$1.00 4½ x 7½; 192 *Nashville, Tenn.*

This interesting book is supposed to be a text for the training of teachers of religion. Its strategy seems to be extremely subtle. There is nothing like a frontal attack on the problem—indeed the book seems almost oriental in its directness. It discusses such matters as endocrine glands, growth, variation of man in stature, and so on. There is an obvious striving throughout towards a scientific viewpoint and attitude of mind. The book is moderate in tone on religious matters throughout.



DEVELOPED LESSONS IN PSYCHOLOGY. *Including Tests with Norms.*

By H. Meltzer and E. M. Bailor.

Harcourt, Brace and Co.

\$1.50 5 x 7½; x + 199 *New York*

The authors have had the brilliant idea of applying some of the pedagogical principles developed in the study of educational psychology to the teaching of psychology itself.



DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

QU'EST-CE QUE LA MÉDECINE? *suivi de Six Autres Essais.*

By E. Rist. *Masson et Cie*
25 francs 5½ x 9; 236 (paper) *Paris*

These seven essays, so brilliant, so judicious, so intelligent, by a great living master, make a notable contribution to the *belles lettres* of medicine. The titles are: "What is medicine?"; "The diagnosis of diseases of the chest before the invention of percussion and auscultation;" "The beginnings of percussion;" "The progress of medicine;" "Science and art in medicine;" "Some moral responsibilities of the physician;" "The Hippocratic oath." In spite of the apparent diversity of these topics there runs through the whole a unifying red thread. Dr. Rist essays, in these pages, an *apologia* for medicine and physicians. He says truly that medicine and physicians have often been sharply and penetratingly criticised, and he wishes to present the other side of the case. He thinks that he is likely to be exonerated of any charge of being a biassed witness because he himself is a physician, on the ground that his defense of medicine and its practitioners will perhaps be relished least of all by physicians themselves.

This book should be translated into English. Surely enterprising American publishers will not miss such an opportunity.

SCIENCE AND THE UNSEEN WORLD.

By Arthur S. Eddington. *The Macmillan Co.*
\$1.25 4½ x 8; 91 *New York*

As in the latter chapters of his "Nature of the Physical World" noted in these columns in a previous issue, the author expands his thesis that science is not enough. There is a realm of experience that can not be comprehended in the symbols of science.

There is an hour of the Indian night, a little before the first glimmer of dawn, when the stars are unbelievably clear and close above, shining with a radiance beyond our belief in this foggy land. The trees stand silent around one with a friendly presence. As yet there is no sound from awakening birds; but the whole world seems to be intent, alive, listening, eager. At such a moment the veil between the things that are seen and the things that are unseen becomes so thin as to interpose scarcely any barrier at all between the eternal beauty and truth and the soul which would comprehend them.

Science can not deny the reality of this clearly felt, unseen world; science has ceased to identify the real and the concrete even in its own domain of physics. In this unseen world, religion and God somehow have play, but Eddington is a Quaker and does not advocate any credal doctrine of what God is or how he works.

As a statement of the religious faith of a great contemporary scientist, the book has some significance, but hardly so as a contribution to religious or metaphysical philosophy. Religion has no special sanction over any profane aestheticism so far as is revealed here, and the logic of the author's reasoning is frequently dubious.



PROCESS AND REALITY. *An Essay in Cosmology. Gifford Lectures Delivered in the University of Edinburgh During the Session 1927-28.*

By Alfred N. Whitehead.

The Macmillan Co.
\$4.50 5½ x 8½; xii + 545 *New York*

In these Gifford Lectures Professor Whitehead has developed and extended his organism philosophy. Further he has matured it. So far as his readers are concerned his views on organism as a fundamental philosophical point of departure were presented in what may perhaps fairly be called an adolescent condition in *Science and the Modern World*. In the present book they are as if grown up, and certainly they are made to do a man's work. For here Whitehead does what he says all truly constructive philosophy must do; namely, having set up a system of ideas, it must "unflinchingly . . . explore the interpretation of experience in terms of that scheme." *Process and Reality* is no minor effort. It is an attempt to enquire into the nature of things on a cosmical scale of

comprehensiveness. The book is difficult, but it will be profitable reading for the biologist.



THE AMERICAN ILLUSTRATED MEDICAL DICTIONARY. *A Complete Dictionary of the Terms Used in Medicine, Surgery, Dentistry, Pharmacy, Chemistry, Nursing, Veterinary Science, Biology, Medical Biography, etc., with the Pronunciation, Derivation, and Definition.*

By W. A. Newman Dorland.

W. B. Saunders Co.
Philadelphia

\$7.00 net, flexible binding, plain

\$7.50 net, flexible binding, thumb index

6 x 9; 1427



THE QUARTERLY REVIEW of BIOLOGY



EVOLUTION OF FACIAL MUSCULATURE AND CUTANEOUS FIELD OF TRIGEMINUS

PART II

By ERNST HUBER

Department of Anatomy, Johns Hopkins University

VII. THE FACIAL TACTILE VIBRISAE IN THE LOWER PRIMATES. EVOLUTION OF MIMETIC MUSCULATURE AND FACIAL EXPRESSION IN THE ASCENDING SCALE OF PRIMATES UP TO MAN. EMBRYOLOGICAL DEVELOPMENT OF THE HUMAN FACIAL MUSCULATURE. RACIAL DIFFERENCES IN FACIAL MUSCULATURE AND FACIAL EXPRESSION

THE *Prosimiae* (lemurs and *Tarsius*) have retained the primitive marsupio-placentalian ground plan of facial tactile vibrissae which can be moved by contraction of voluntary muscles of the facial group. In the lemurs (fig. 28) facial tactile sense, together with well developed sight and hearing, evidently plays a guiding rôle. Also for *Tarsius* (fig. 29) this facial tactile sense is a valuable addition to the highly evolved sight and hearing.

Within the *Simiae* in the most primitive forms, represented by the lower platyrrhine monkeys, such as the Hapalidae (fig. 30), and *Nyctipithecus* (*Aotus*) (fig. 31a and b) among the Cebidae, the tactile facial

vibrissae are arranged in a way very similar to that in *Tarsius*. They have, however, undergone further reduction. As to the superficial facialis musculature the marmosets and *Aotus* show a primitive ground plan similar to that of *Tarsius*, if we disregard the specializations in the latter. But there are other striking simian features which the marmosets and *Nyctipithecus* share with the higher platyrrhines and lower catarrhines. The functioning of the superficial facialis muscles as mimetic musculature in the Hapalidae and the primitive Cebidae is still on a very primitive level. Indeed, these lowly primates have little facial expression.

As we ascend in the "simian scale" we notice that facial tactile vibrissae cease to be essential structures. They still persist, however, as vestigial sinus hairs, in the supraciliary region, not localized there, however, in a single patch, as in the lower platyrrhines, prosimians and the rest of the placentals and the marsupials, but secondarily scattered over the entire supraorbital margin; facial vibrissae are moreover found on the upper and lower lips.

It is noteworthy that those facial muscles (*M. depressor supercilii*, *M. maxillo-naso-labialis* (in part), *M. mentalis*), which in the primitive primates move the well developed facial vibrissae, presumably having evolved in close correlation with this tactile apparatus, persist in the higher primates, despite the deterioration of the tactile vibrissae. They are, however, modified structurally and have altered function.

The deterioration in the higher primates of an originally important tactile mechanism, is obviously in close correlation with the further elaboration of the visual apparatus, with the evolution of the anterior extremity, especially the hand, and, in the case of the higher platyrrhines, with the acquisition of a prehensile, sensitive tail (see also Wood Jones and Porteus, 1928; Tilney, 1928, and others). By combined use of their eyes, hands and prehensile, sensitive tail these primates possess a much fuller orientation in their surroundings. This great improvement in the organization must have been an important factor in the further evolution of the neopallium, which brought higher intelligence,—a development which is also reflected in a more elaborate facial expression of these primates. Elaboration of facial expression goes hand in hand with a further differentiation of the mimetic musculature (fig. 31c and d contrasted with fig. 31a and b) and the involved central nervous mechanism.

In the lower catarrhines, as the macaque (fig. 32) for example, facial expression is still largely stereotypical. The gibbons (fig. 33) are intermediate between the lower catarrhines and the great anthropoid apes. In the great anthropoid apes the elaboration of the central nervous mechanism, including the differentiation of the facial area of the motor cortex, has reached a higher degree than in the gibbon and the

lower catarrhines (compare chapter III). Side by side with this goes a further differentiation of the mimetic musculature (figs. 34, 35 and 36). This gave the basis for a more complex though still rather crude grimace-like facial expression. Nevertheless a large range of individual features of expression is noticed in these highly intelligent animals (compare Yerkes' *Almost Human*, 1925).

In *man* facial expression has finally reached marvelous perfection. This phenomenon may be attributed to further differentiation of the mimetic musculature (compare figs. 39-46), in close correlation with higher evolution of the central nervous mechanism, i.e. further development of the facial area in the motor cortex and through elaboration of the association centers.

Taking into consideration the fact that spontaneous facial expressions with their manifold delicate shadings result from varied emotional reactions, we may conclude that the elaboration of facial expression during the phylogeny of man closely followed the evolution of emotional life, which in turn depended on the elaboration of the association centers. We may further assume that evolving man consciously used and developed certain facial expressions in order to make himself understood by his fellow creatures in a fuller and more definite way. We still notice occasionally in modern man imperfect functioning of one or another of the mimetic muscle groups. Thus additional muscles may contract when the contraction of a limited group is intended by the individual. There are occasional individuals who cannot contract the superciliary and glabellar muscles without at the same time tightly closing the eyes with the *M. orbicularis oculi*. This phenomenon is presumably a persistence of a phylogenetically older, less differentiated pattern. Through special

effort and with continued practice, however, such persons may succeed in eliminating the associated contraction of the *M. orbicularis oculi*, thereby perfecting the independent play of the *Depressor supercilii-corrugator-procerus-nasi* muscle group, as is ordinarily done in frowning. We may assume that through such a process of gradual functional perfection finely graded facial expression has evolved from a lower stage, where crude, grimace-like group action of mimetic muscles prevailed as in the facial expression of the anthropoid apes and lower primates. There can be no doubt, moreover, that the acquisition and gradual perfection of articulated language has had a further decisive influence in the evolution of the mimetic musculature and facial expression.

It should be emphasized that the individual mimetic muscles lack a well defined muscle fascia, in contrast to the skeletal muscles, in which the bundles are solidly bound together into compact structures by such fasciae. Hence, in the case of the mimetic musculature, smaller muscle portions, even single muscle bundles, may contract independently of the rest of the muscle,—this in manifold combinations with synergetic muscle portions within functional muscle groups. The richly branched facial nerve affords the necessary motor innervation to these various muscle portions.

Moreover, it is significant that the coherent superficial body fascia, although it covers as a thin sheath the pars colli of the platysma, does not extend into the face. A fascial cover, like a veil spread over the delicate, thinly bundled mimetic musculature, would of course make elaborate facial expression impossible. The mimetic muscles lie directly subjacent to the freely movable skin. There the inserting muscle bundles are anchored in the subcutaneous tissue, or firmly attached to the cutis itself.

The latter method of attachment holds in the superciliary region, in the naso-labial fold, over the chin, and in the lips. Under the influence of the contracting mimetic muscles the elastic skin is laid into folds, which as a rule are at a right angle to the direction of the muscle bundles. Since, in compound facial expression, series of muscle portions with different bundle directions are simultaneously set into action, the wrinkling of the skin becomes complex. In those areas where the muscle bundles insert directly into the cutis, muscle contraction brings forth, not wrinkles, but grooves or dimples. Individual muscle variations, differences in thickness of the cutis and subcutaneous tissue and differences in the elasticity of the skin naturally have modifying influences, thus adding to the individuality of facial expression.

Detailed studies of the morphology of the human mimetic musculature with careful consideration of the innumerable individual variations afford evidence for the view that evolution of the central nervous mechanism preceded the evolution of this muscle apparatus. The superficial muscle complex in the temporal region, the *M. occipitalis* and the entire ear musculature in man are found in a stage of progressing degeneration. The functional deterioration has gone further than the structural degeneration. While many, perhaps most persons still possess the ability to control the *M. occipitalis*, those are fewer who are still capable of contracting the extrinsic ear musculature in attempts to move the ears. It is usually the *M. auricularis posterior* which can be contracted if set into action jointly with the *M. occipitalis*. These two muscles form an old phylogenetic and functional unit. Still rarer are the persons who are able to contract the *M. auricularis posterior* alone. Such action is usually accompanied by an increased

innervation of the *M. occipitalis*, which is appreciated by tightening of the galea aponeurotica. Rare, indeed, are the individuals who can set into action the *M. auricularis anterior et superior*. In the intrinsic ear musculature, the functional deterioration evidently has progressed still further. It is very doubtful whether any of these little muscles can be voluntarily moved at all, although they persist as well defined muscle masses with apparently intact nerve supply.

In contrast to the evident deterioration of the above named groups of the superficial facial musculature, we find the musculature of the face proper, the "mimetic muscles" in the strict sense, in a state of progressive development. This musculature has by no means reached an end stage of evolution. We can not fail to recognize in certain of these groups a trend towards fuller differentiation into distinct individual muscles. Thus evolution seems to be still intensely at work in the muscle field of the glabellar and supraorbital region and in the musculature about the mouth. We encounter in these areas all possible transitions from very primitive conditions with persisting old phylogenetic muscle connections, to progressive states, where the individual muscles are more clearly differentiated. It is in these areas with the most highly differentiated muscle groups that the most vivid facial expression is noticed. In some individuals the musculature around the eyes and in the glabellar region is more responsive, while in others the musculature about the mouth becomes outstanding in facial expression. Often both groups are equally responsive. It is interesting to see that in man the functional perfection of the mimetic musculature has progressed much further than the structural differentiation of this muscle field.

In connection with the study of the

morphology of the mimetic musculature, investigations on representatives of races other than the white are of great interest. The very active period of *racial anatomical research* during the first three decades of the twentieth century considerably furthered our knowledge of the mimetic musculature in various races of the human stock, especially of "Negroes," Papuans and Melanesians, Australians, Malays, Chinese, Japanese, Indians, in contrast with the Whites.

The author had the opportunity to investigate a large series of American Negroes (fetuses, new-born, children and adults of both sexes), and to compare them with the White, with an adult Chinese and an adult Hawaiian (figs. 39-46). Through these studies he could support and supplement former authors, among them the pioneer Chudzinski, who was the first to keenly appreciate racial differences in the mimetic musculature and in the rest of the muscle system. It appears astonishing that a series of authors, some notable authorities, are still sceptical as to the occurrence of racial anatomical differences in the soft parts, including the muscle system. Yet more and more convincing data are brought together proving the existence of such racial differences. According to the author's experience the racial characteristics are more conspicuous in the mimetic musculature than in the rest of the muscle system, where racial differences are likewise recognizable. It is to be noted that these differences appear early in fetal life (compare fig. 40).

A vast amount of valuable data on the racial anatomy of the mimetic musculature has been obtained through the researches of many authors (see bibliography).

Although *attempts to analyze and explain facial expression in man* are very old the extensive literature on the "Science of Physiognomy," especially the older, is full

of worthless statements and fantastic speculation. However, a series of publications on facial expression initiated by the classical works of Bell and Darwin is on a sound morphological basis. Yet hardly more than a beginning has been made in broadly correlating facial expression with neuro-physiology. To quote just a few historically important or otherwise valuable and fundamental works in this field I refer to Lebrun, 1667; Camper, 1774, 1791; Lavater, 1775/78; Bell, 1806; Duchenne, 1861; Gratiolet, '65, '72; Piderit, '67; Darwin, '72; Wundt, '77; Birch-Hirschfeld, '80; Montegazza, '90; Bugnion, '95; Rudolph, 1903; Virchow, '08; Krukenberg, '22; Lightoller, '25, '28.

While in the evolution of facial musculature and facial expression during the phylogeny of man, the elaboration of the central nervous mechanism evidently precedes the structural differentiation of the mimetic muscles, this is not the case in the *individual development*. The mimetic musculature receives its structural differentiation very early in fetal life. The critical period of development and differentiation is between the second and third month (fig. 39). In the three months' fetus (fig. 39d-f) this muscle field is already regionally differentiated, and the principal branches of the facial nerve are formed (Huber). Up to the fifth month (figs. 40, 41a), however, the mimetic muscles are found to be rather delicate and of gelatinous, half transparent consistency, which renders their dissection and study difficult. From this period on (fig. 41b and c) the muscle bundles receive their final structural differentiation and characteristic reddish coloring, and the proportions of the individual muscles become more and more those of the new-born, illustrated in figures 42 and 43a.

Postnatal changes are slight. The mimetic muscles grow in proportion to the

whole head, while the growth of the masticatory musculature on the other hand goes side by side with the growth of the mandible, which is largely determined by the dentition. It is noteworthy that the two muscle groups, the mimetic and the masticatory musculature, which are situated so closely together, develop at a very different rate.

In contrast to the completed structural differentiation of the mimetic musculature and corresponding peripheral facial branches at birth, there is practically no *facial expression* in the new-born. Expression evolves very gradually in connection with the completion of the development of the sensory mechanisms and with the elaboration of association centers. As the young infant's conscious and intelligent reactions to the surrounding world grow, facial expression becomes more manifold and more definite. There is remarkable progress during the first year, and the second and third years bring further elaboration (compare also Buchner, Preyer, Bugnon, Krukenberg *et alii*). Facial expression resulting from emotional reactions (upon adequate external stimuli or upon associations of ideas, which revoke memories of past experience), remains unmasked through childhood. It is thus possible to read in the child's face the true meaning of the manifold expressions with all their rich modulations.

Facial expression is evidently a highly complex reflex action, in which the highest cortical centers are involved. Certain impulses arising in association centers, reach the facial area of the motor cortex and, when sufficiently strong, they seemingly release, against our will, motor impulses to the mimetic muscles. While a person is awake, the mimetic muscles, like the rest of the voluntary muscle system, are kept in a state of tonus, ready to contract at any time. Yet the intensity of tonus varies

according to the state of attention of mind. It varies from person to person. Motor impulses which reach the mimetic muscles may simply increase this tonus, or they may set the various functional groups into

mimetic musculature goes the expression in the eyes, a mechanism which would deserve special discussion. As regards facial expression it should be emphasized that spontaneous contraction of voluntary

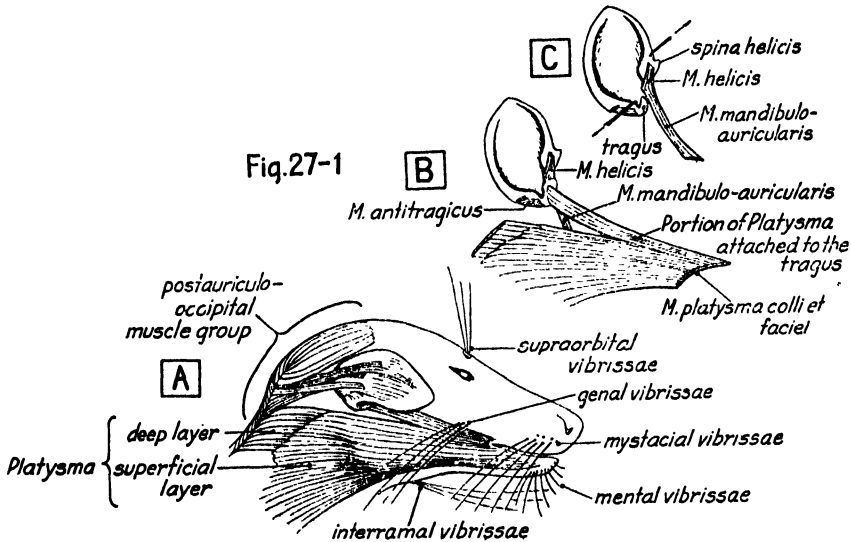


FIG. 27. SCHEME OF THE PRIMATE GROUND PLAN OF SUPERFICIAL FACIAL MUSCULATURE AND FACIAL TACTILE VIBRISSAE, FOR THE UNDERSTANDING OF THE FOLLOWING SERIES OF UNLABELLED FIGURES REPRESENTING FUNDAMENTAL TYPES OF THE "ASCENDING SCALE OF PRIMATES" (compiled from the actual findings in the lemurs, *Tarsius* and lower platyrrhine monkeys)

Fig. 27-1. *The Platyisma and its Derivatives*

A. The Platyisma is seen in a primitive arrangement, arising with a deep layer from the nuchal region as in the original marsupio-placental ground plan of fig. 6, part I, while the "primitive sphincter colli," the matrix of the entire superficial facial musculature (compare fig. 6), has dropped from the primate ground plan. The postauriculo-occipital muscle group (*M. occipitalis*, part of the extrinsic and intrinsic ear muscles) with the nuchal portion of the platysma remained in primitive connection. The deep and the superficial layers of the platysma unite to build the uniform plate of the *M. platysma colli et faciei* (compare also fig. b). The most caudal bundles of this muscle deviate towards the shoulder region. Note the full set of well developed *facial tactile vibrissae* in an arrangement characteristic of the original marsupio-placental ground plan of fig. 23, part I.

B. The *M. platysma colli et faciei* is joined by a muscle band (*M. auriculo-labialis inferior*, Ruge), which posteriorly attaches itself to the tragus of the ear. On the ear cartilage note the *M. antitragicus* and *M. helix*, muscles of the postauricular group, which have migrated from the posterior to the anterior surface of the ear, while the *M. mandibulo-auricularis* has still further intruded into the preauricular muscle territory by migration along the cartilaginous ear tube, towards the mandible, where it has gained attachment.

C. Anterior and posterior borders of the ear cartilage are here shown pulled a little apart in order to demonstrate the primitive connection of the *M. helix* with the *M. mandibulo-auricularis*. The latter is represented as cut off from the mandible below.

Besides the muscles shown in the figures a-c the platysma gave rise in the higher primates to the *M. quadratus labii inferioris* and to the *M. rectus labii inferioris*. The rest of the superficial facialis muscles, including some of the extrinsic and intrinsic preauricular ear muscles, and the large bulk of the muscles of the face are derived from the *Sphincter colli profundus*.

contraction. Spontaneity, intensity and extent of these contractions are graded by the intensity of psychic impulses. Parallel with facial expression through the

muscles upon emotional stimuli is a motor reaction largely characteristic of the facial field.

With increasing experience and under

the influence of education, the maturing individual learns to control spontaneous facial expression, and thus succeeds, to varied degree, in concealing emotions.

taneous response of the facial field, are counteracted or modified by a complex association mechanism before they reach the facial area of the motor cortex. As a

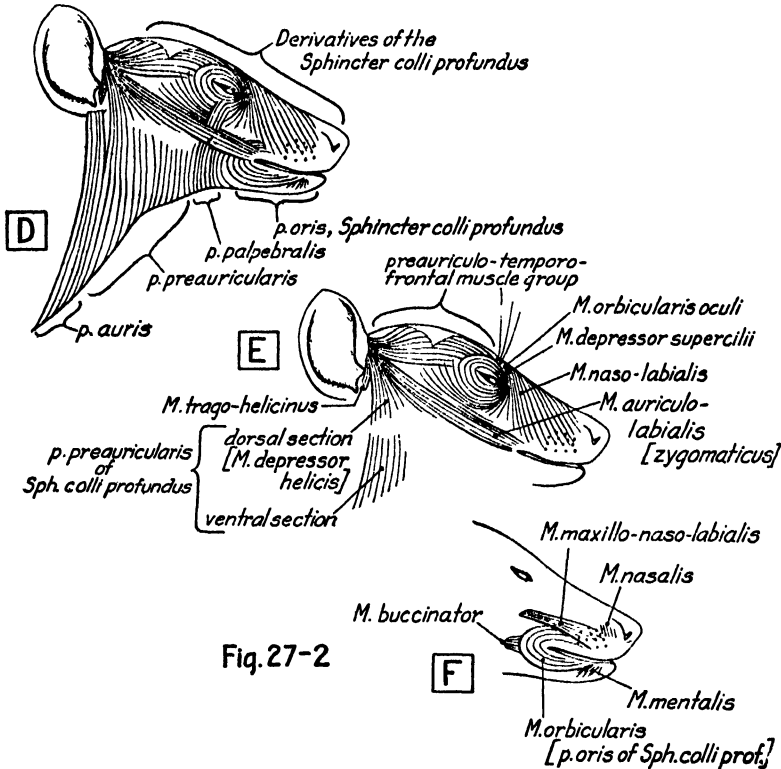


Fig. 27-2. The Sphincter Colli Profundus and its Derivatives

D. The primitive arrangement of the *Sphincter colli profundus* represented by a continuous transverse layer, which extends from the ear to the mouth cleft, as in the original marsupio-placental ground plan of fig. 6, part I. While the most caudal section of the *Sphincter colli profundus*, the *pars auris*, inserts into the ear cartilage close to the incisura intertragica, the *pars preauricularis* of the *Sphincter colli profundus* has gained attachment to the helix of the ear. From here muscle portions have expanded over the upper part of the face, giving rise to a series of more or less distinct individual muscles. The derivatives of the *pars preauricularis sph. colli profundus* include the *M. trago-helicinus*, the preauriculo-temporo-frontal muscle complex, the *M. orbicularis oculi*, *M. depressor supercilii*, *M. naso-labialis*, and *M. auriculo-labialis* (*zygomaticus*). These muscles are once more represented in fig. e, where the dorsal section of the *pars preauricularis* (*M. depressor helicis*) *sph. colli profundus* is shown disconnected from the ventral section, which has remained part of the continuous layer of the *Sphincter colli profundus*.

The *pars palpebralis* of the *Sphincter colli profundus* (fig. d) inserts above into the lower eyelid, thus forming a *M. depressor palpebrae inferioris*. Anteriorly the *p. palpebralis* is continuous with the *p. oris*.

The *pars oris*, the most anterior part of the *Sphincter colli profundus* (fig. d) has given rise to the musculature of the snout, lips and cheek wall, as shown in fig. f, where the overlying *M. naso-labialis* has been removed. The derivatives of the *pars oris* are: *M. orbicularis oris*, *M. buccinator*, *M. maxillo-naso-labialis*, *M. nasalis* and *M. mentalis*. Additional individual muscles have arisen from this group in the higher primates.

We may assume that through this educational process emotional impulses, which in the child would invariably cause sponta-

neous response of the facial field, are counteracted or modified by a complex association mechanism before they reach the facial area of the motor cortex. As a

result of this, reading the face of adults becomes difficult. It is true that we can, at any time, set

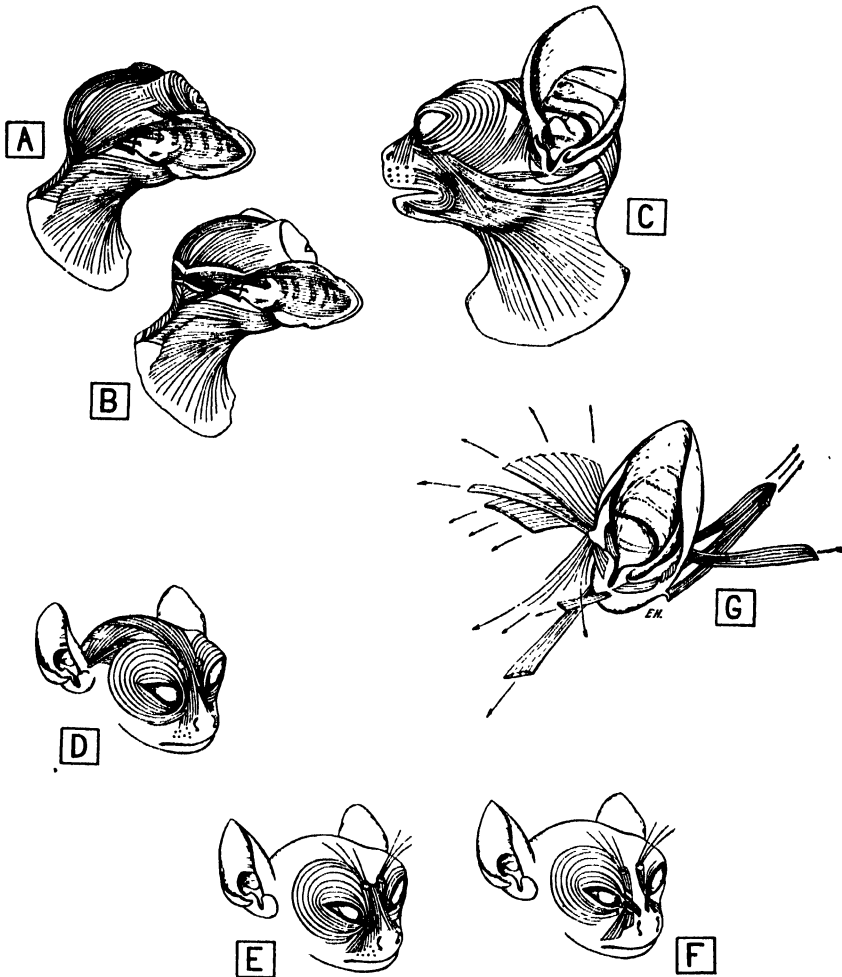


Fig.29

FIG. 29. *TARSIVUS SPECTRUM* (A, B, D, E, F) AND *T. SALTATOR* (C, G), THE LATTER SOMEWHAT ENLARGED COMPARED WITH *T. SPECTRUM* (BOTH OF THE JOHNS HOPKINS ANATOMICAL COLLECTION)

The superficial facial musculature, practically identical in the two species is specialized on a primitive, distinctly prosimian plan (Huber).

Figs. 29*a* and *b* show the platysma in an almost schematically primitive arrangement, arising with the deep bundle layer from the nuchal region (ligamentum nuchae, processus spinosi of the lower cervical and upper thoracic vertebrae). Fusing with the superficial bundle layer it forms the *M. platysma collis et faciei*, which is seen in its full extension in fig. *c*. In the nuchal region the postauriculo-occipital muscle complex remained in primitive connection with the origin portion of the platysma (figs. *a* and *c*). The post-auriculo-occipital complex is differentiated into a series of individual muscles, some of which have shifted their origins cranialward to the occiput (fig. *b*), as in *Lemur* (compare fig. 28*a*). The *Mm. obliqui et transversi*, which are derived from the extrinsic postauricular muscles, are extremely well developed. They cover practically the whole convex surface of the ear cartilage (figs. *a* and *b*), here bridging the grooves, which correspond to the four transverse ridges of the concave surface of the ear cartilage (compare figs. *c* and *g*).

The guiding senses of *Tarsius* are sight and hearing, with the auxiliary muscle apparatuses accordingly evolved and highly specialized along distinct lines peculiar to this genus. The powerful *M. orbicularis oculi* (figs. *c*, *d*, *e*, *f*), which protects the unusually big eyeballs, is noteworthy. The *M. orbicularis oculi* shows specializations (fig. *f*) nowhere else encountered in the order of the primates. Characteristic also is the conspicuous *M. depres-*

getic contraction of muscles the naso-labial fold, where the most powerful of these muscles insert, is deepened, the mouth is forced open and the smile turns into a happy, hearty laugh.

For these fine modulations of expression in the face of the White, a readily responsive neuro-mechanism, rather well differentiated, not too massive mimetic muscles (fig. 43) and a not excessively thick, elastic skin constitute the necessary basis. Naturally variations of the involved individual muscles, of the skin and subcutaneous tissue, and additional contraction of further muscle portions, e.g. in the region about the lateral angle of the eyes, over the back and lateral surface of the nose, greatly add to the individuality of expression in different persons.

Could we expect to find equally fine modulations of expression in the face of the *Negro*? The less differentiated, coarsely bundled mimetic musculature typical of the *Negro* referred to above (fig. 44a) and the greater thickness of the skin make this improbable. In fact there is a marked difference in facial expression compared with the White. But this is by no means due alone to the structural difference of the involved mimetic musculature and to the increased thickness of the skin, but probably more to the difference in functioning of the neuro-mechanism. Apparently

less finely graded nerve impulses reach the respective mimetic muscle groups, thus setting them into sudden, strong contraction which rather suggests more primitive muscle actions. The expression is characteristic. Through the strong "labial tractors," especially through the undifferentiated Zygomaticus muscle-mass, the bulky lips are vigorously pulled upward and outward, so that the set of large-sized white teeth show up in contrast to the dark colored face. Instead of a graded laughing typical of the white we notice the characteristic grinning of the *Negro*. And through often simultaneously uttered sounds which differ in color of voice from those of the White, the *Negro's* grinning becomes even more characteristic.

The *Polynesians*, a highly intelligent race, dark skinned, like the *Negroes*, yet somatically and in regard to their psychology profoundly different,—show a distinctly different facial expression, similar to that of the White. I shall never forget the intelligent, pleasing and charming features of the kindly Hawaiian faces.

Very different again is the facial expression in representatives of the *Mongolian stock*. The schematic facial expression of the *Chinese* and *Japanese* is striking. For White people there is, at first, little individuality noticeable in those *Mongolian* faces. The expression seems rather indif-

cor palpebrae inferioris (fig. c), which represents a powerful synergist to the *M. levator palpebrae superioris* of the oculo-motor group. With these two muscles as antagonists to the *M. orbicularis oculi* *Tarsius* may keep the eyes wide open.

The outer ear with the auxiliary muscle apparatus is highly perfected. Not less than ten distinct extrinsic ear muscles insert from different directions into the huge, spoon-shaped ear cartilage (fig. g). Well defined intrinsic ear muscles are supplied to adjust the entrance of the ear tube to incoming sound waves, and there are additional peculiar modifications of the ear cartilage. Thus the anthelix (*plica principalis*) is developed into a large shield (fig. c). There are, moreover, four transverse ridges on the concave surface which may be rendered more prominent through contraction of the above mentioned *Mm. obliqui et transversi*. And there is a little basket-shaped structure lodged on the lateral border of the scapha. All these are structures by which sound waves from practically every direction may be collected, and reflected into the ear tube. In the elaboration of the auxiliary apparatus to the visual and auditory mechanisms,—marvelous adaptations to exclusively nocturnal life,—*Tarsius* far excels the *lemurs*.

The facial tactile vibrissae, with the exception of the interramal group, are still distinct in *Tarsius* though not as conspicuous as in *Lemur*. Among the muscles which control these vibrissae the *M. depressor supercilii* is even more highly evolved than that of either *lemurs* or any representative of the simian stem. Through secondary fusion with a modified deep portion of the *M. naso-labialis* (figs. e and f) it has gained a broad bony attachment below on the maxilla (fig. f), an acquisition which renders this little muscle more efficient.

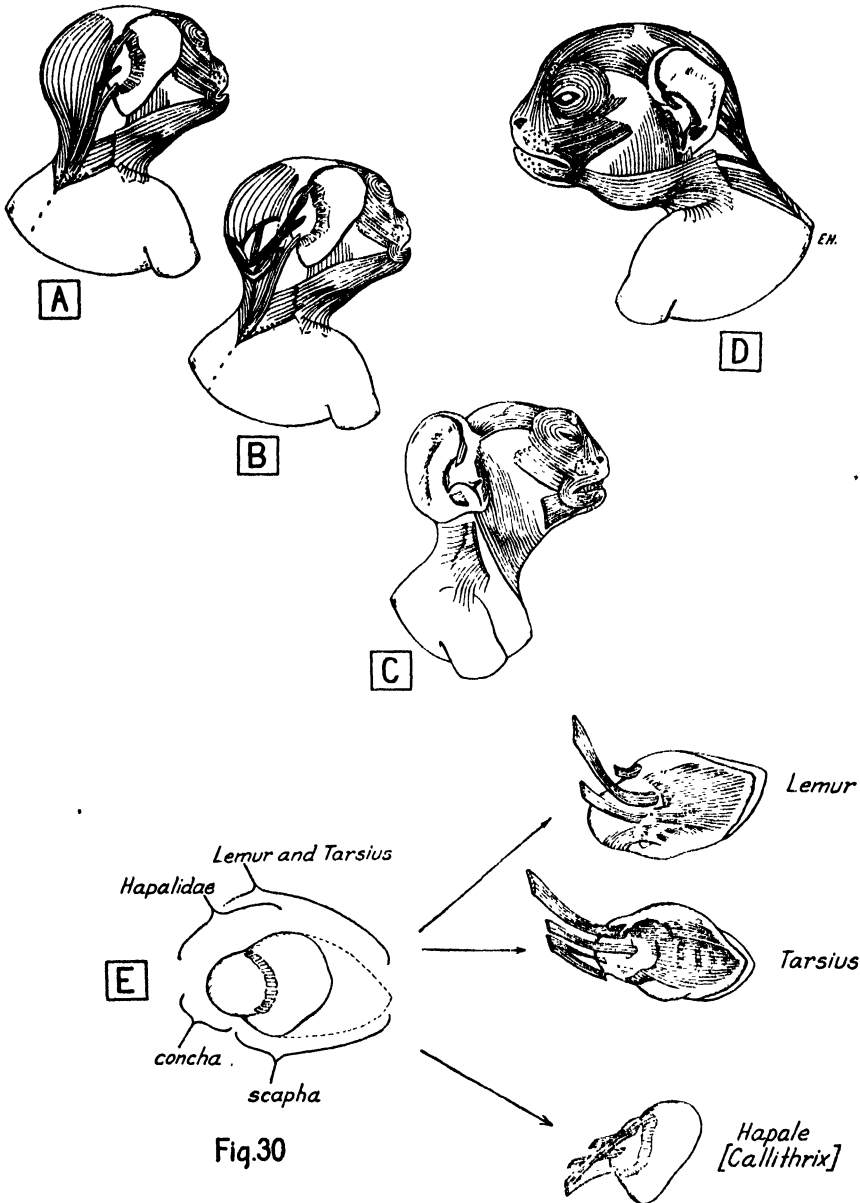


FIG. 30. *HAPALE* (*CALLITHRIX*) JACCHUS (FIGS. A-C) AND *LEONTOECHUS* (*OEDIPOMIDAS*) GEOFFROYI (FIG. D) AS REPRESENTATIVES OF THE *HAPALIDAE* (MARMOSETS), THE MOST PRIMITIVE PLATYRRHINE MONKEYS (JOHNS HOPKINS ANATOMICAL COLLECTION)

The plan of the superficial facial musculature, practically identical in the two genera (compare also Ruge, 1887, and Schreiber, 1928), resembles that of *Tarsius*, if we disregard the specializations in the latter. Thus the platysma shows the same primitive extension, and the postauriculo-occipital muscle complex has likewise remained in primitive connection with the deep bundle layer of the platysma (figs. *a* and *b*). It is less differentiated and less specialized than in *Tarsius*; deep portions, however, (fig. *b*) have already shifted to the occiput, as in *Tarsius*.

ferent and the whole mimetic musculature appears to be in a stage of relaxation. Upon more careful analysis of single individuals one becomes aware, however, that Chinese and Japanese are capable of a far greater range of facial expression than we are accustomed to assume. These elements of expression represent, in part, characteristic features of their own. As to the expression of emotions we recognize that happy outbursts are expressed by these Mongolians through controlled smiling rather than real laughing. Through conservative, rather rigid education facial expression in the Chinese and Japanese is apparently suppressed. This view is supported by the fact that Chinese and Japanese who have lived long enough in countries with a prevailing white population in Western civilization show more spontaneity in their facial expression. They often become aware of this fact themselves, as I gathered in a series of cases.

Like the Chinese and Japanese the self-possessed, stolid *American Indian* shows little spontaneous facial expression, but through his mimetic musculature goes a strong tonus, which gradually brings out

the sharply cut, keen traces so characteristic of many Indian faces. The *Eskimo*, on the other hand, gives a much more vivid response. Indeed through their spontaneous facial expressions, the Eskimoes show that they are a happy folk, despite their continuous hard struggle against the unfavorable elements of the far North.

From the preceding discussion it becomes evident that the analysis of facial expression of man involves most intricate problems. The solution of these problems requires closely correlated studies on the evolution of the mimetic muscles in the ascending scale of the Primates with emphasis on the large range of individual and racial variations in man, and on the gradual evolution of the complex neuromechanism. Of highest importance, and most difficult, is the analysis of the psychic component during the development from the new-born to the adult within the various human races. It should moreover be kept in mind that language may possibly have a modifying influence. Analysis, with the slow motion picture, of the muscle activity involved in uttering the various sounds during speech, shows the

The *Sphincter colli profundus* (figs. c and d) has retained its primitive extension, and the *M. depressor bulicis* in front of the ear remains part of the *Sphincter colli profundus* layer (compare also Schreiber, '28), while in the Lemuroidea and *Tarsius* on the other hand this muscle has been freed from its matrix. This very primitive condition in the marmosets is noteworthy. It proves that the preauricular musculature, the orbito-temporo-frontal muscle complex, *M. orbicularis oculi*, *M. depressor supercilii*, *M. nasolabialis* and *M. auriculo-labialis* (*zygomatikus*), together with the musculature of the lips and cheek wall, are indeed derivatives of the *Sphincter colli profundus* (Huber, compare chapter I) and not of the platysma (Ruge, 1885, '87).

In contrast to the Lemuroidea and *Tarsius*, there is in the marmosets no secondary fusion of the platysma with the muscle portion corresponding to the *M. auriculo-labialis* (superior) of the Prosimiae. While this latter muscle in the marmosets has retained its broad primitive connection with the *M. orbicularis oculi* (figs. c and d), it is reduced in its preauricular section, thus forming a *M. zygomatiko-orbitalis*, which the marmosets share with the rest of the Simiæ. The distal portion of the ear cartilage is considerably reduced in comparison with that of *Lemur* and *Tarsius*.

Fig. e shows the ear cartilage (viewed from the convex surface) with the extrinsic and intrinsic ear muscles in *Hapale* (*Callithrix*) contrasted with *Lemur* and *Tarsius*. The comparison shows strikingly how much indeed in *Hapale* the scapha portion of the ear cartilage has become reduced. The *Mm. obliqui et transversi*, which in *Lemur* and *Tarsius* cover practically the entire convex surface of the ear cartilage, in *Hapale* form a small zone of muscle bundles, which bridge the fissure between concha and scapha, a cleft known as *sulcus antheliciis transversus sive fissura plicae principalis* (Boas). The plan of the ear musculature in the marmosets is not only simpler than that of *Tarsius* and the Lemuroidea, but it is secondarily reduced through deterioration of the *Mm. obliqui et transversi*, and through the loss of the *M. mandibulo-auricularis*, a muscle which belongs to the original marsupio-placental ground plan (compare Huber, 1918-26) and which is retained as an essential, functioning muscle in the prosimian plan. The marmosets, in contrast to the Prosimiae, share these characteristics with the rest of the Simiæ.

The tactile apparatus of facial vibrissæ (in figures indicated clipped off) shows a similar arrangement to that of *Tarsius*; however, in addition to the interramal vibrissæ the marmosets have lost also the genal vibrissæ.

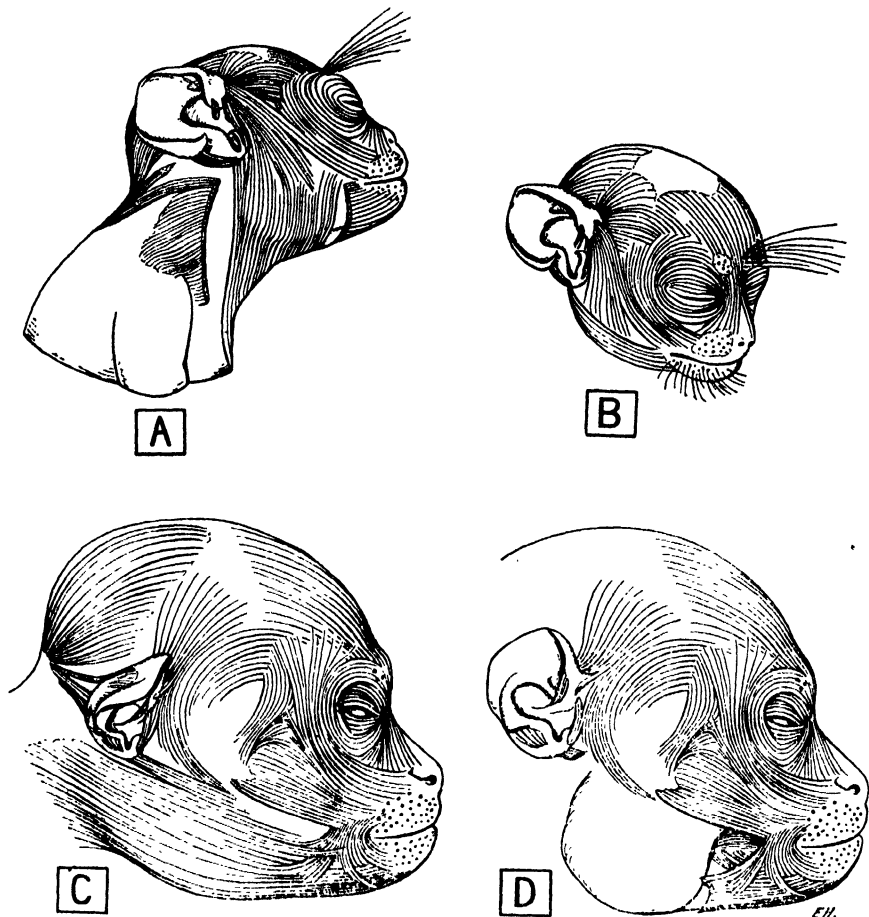


Fig.31

FIG. 31. *NYCTIPITHECUS* (*AOTUS*) AND *ATELES ATER* (SPIDER MONKEY), THE FORMER A PRIMITIVE AND THE LATTER A HIGHLY EVOLVED AND SPECIALIZED REPRESENTATIVE OF THE CEBIDAE, THE SECOND FAMILY OF THE PLATYRRHINES (COLLECTION OF DIVISION OF MAMMALS, U. S. NATIONAL MUSEUM, AND JOHNS HOPKINS ANATOMICAL COLLECTION)

Nyctipithecus (figs. a and b) is interesting in that it combines primitive characteristics of the Prosimiae and of the lower platyrrhines. In some regards it is more primitive than the Hapalidae, while in others it is intermediate between the Hapalidae and the Higher Cebidae. Note in fig. a the primitive extension of the *sphincter colli profundus* and its primitive connection with the preauricular muscle complex and the *M. auriculo-labialis* (*zygomaticus*). It is also noteworthy that in *Nyctipithecus* the conspicuous supraorbital tactile vibrissae are concentrated in one single bundle over the medial end of the margo supraorbitalis. There they are implanted into a wart-like projection of the skin (fig. b), into which bundles of the *M. depressor supercilii*, *M. orbicularis oculi* and *M. frontalis* are inserted. By this characteristic arrangement of the supraorbital vibrissae the Prosimiae, Hapalidae and *Nyctipithecus* contrast with the higher platyrrhines and all the catarrhine monkeys, apes and man, where the Supercilii are found scattered from the lateral end of the supraorbital margin to the glabella (compare e.g., fig. 33: gibbon).

Ateles (figs. c and d) has the facial musculature evolved to a considerably higher level than *Nyctipithecus*. Through deterioration of the nuchal portion of the platysma the postauriculo-occipital muscle group has become independent of its matrix (compare fig. c with fig. a). It has settled down on the occiput. The *M. auricularis posterior*, consisting of several slips, has become more independent of the *M. occipitalis* and has shifted its origin closer to the ear cartilage (fig. c). In striking contrast to the marmosets and *Nyctipithecus*, the *Sphincter colli profundus* in *Ateles* has dropped out from the plan (fig. d); and its derivatives, the muscles of the face, have received further elaboration. The formation of a *M. triangularis*, which overlaps the platysma, is noteworthy (fig. c). The orbicularis oris-buccinator group (only partly shown in fig. d) has likewise evolved above the stage of the lower platyrrhines. *Ateles* shares these progressive features with other representatives of the higher Cebidae, notably with *Alouatta* (*Mycetes*) and *Lagothrix*, while *Cebus* in some respects is a little more primitive (Ruge, 1887; Schreiber, 1928; Huber).

great complexity of synergetic actions of the various muscle portions of the mimetic muscles of the lips and cheek wall (Lightoller, 1925). According to the diverse languages certain portions of these muscles may be involved more vigorously and more frequently in one language, while in another language other muscle portions may be of greater functional importance. It is hence not unlikely that certain peculiar features of expression of the various human races and of subdivisions of these races, depend on differences in the language. If this assumption should prove correct we may further expect that individuals who acquire a new language and practice this over a long period acquiring facility, should gradually show a change in facial expression about the mouth.

If we progress on the lines which I have here briefly outlined we will, I think, gain a fuller understanding of facial expression with its modifications in the various human races. Here lies a vast, rich field for future research.

VIII. THE UNSETTLED QUESTION OF DEEP SENSIBILITY OF THE FACE. NEW EXPERIMENTS EVIDENCING THE EXISTENCE OF POSTURAL SENSE IN THE MIMETIC MUSCULATURE IN MAN, CONDUCTED TOGETHER WITH MUSCLE PRESSURE SENSE BY THE N. FACIALIS

The pathway for deep sensibility of the face has long been disputed. Through clinical and experimental investigations, Spiller (1906), Ivy and Johnson (1907/08), Davis (1923), and Gerard (1923) came to the conclusion that deep sensibility (pressure, pain) of the face is carried in the N. *facialis* and not in the N. *trigeminus*. One may assume that the deep sensibility here in question is transmitted through sensory facial branches which terminate within the facial musculature. It is to be expected that coëxisting with this "deep

facial sensibility" or "muscle pressure sense" there is a sensibility in the deeper layers of the subcutaneous tissue, transmitted through sensory trigeminal branches. Any pressure stronger than a light touch exerted upon the skin over the face would naturally reach the endings of the sensory branches of the N. *trigeminus* in the deeper layers of the subcutaneous tissue, as well as the endings of the sensory branches of the N. *facialis* within the subcutaneously located facial musculature. After elimination of the sensory trigeminus, the deep pressure sense in the facial musculature remains, as demonstrated through the clinical and experimental studies of the above quoted authors, as well as through personal experiments (Huber and Hughson). While in the face "deep skin pressure" sensibility may not be considerable, it surely plays a great rôle in other parts of the body, above all on the palmar and plantar surfaces. This may be deduced from the fact that here the cutaneous nerve branches involved end in complex sense organs, the Pacinian corpuscles, which presumably represent the receptors of "deep skin pressure."

If we exert still stronger pressure upon the skin over the face, this pressure also reaches the sensory nerve endings in the periosteum of the facial part of the skull. No experiments have so far been undertaken to discriminate in the face this "deep, periosteal pressure" from the muscle pressure and the deep skin pressure. It is to be expected that periosteal pressure over the face and anterior part of the cranium is conducted through the N. *trigeminus*, while periosteal pressure over the occipital and mastoid regions should be found through the branches of the N. *occipitalis major* and the corresponding sensory branches of the cervical plexus (N. *occipitalis minor* and N. *auricularis magnus*). Over the vertex, there is probably an

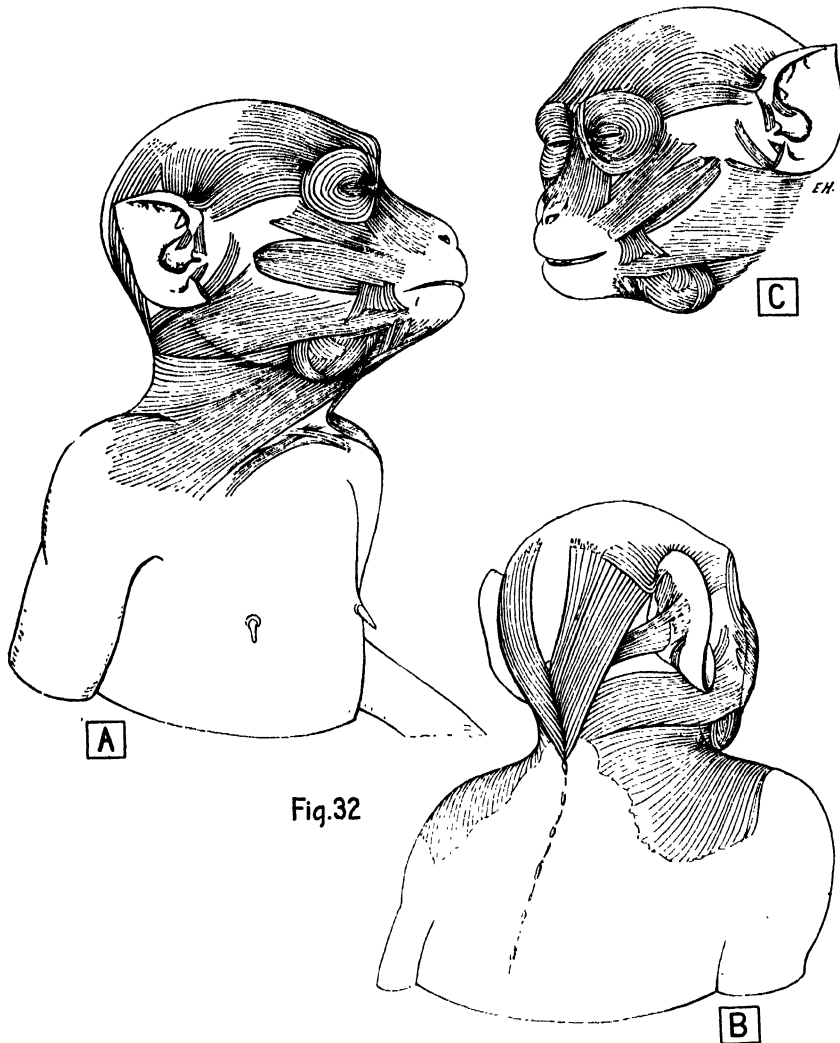


Fig.32

FIG. 32. *PITHECIUS (MACACUS) RHESUS*, AS A REPRESENTATIVE OF THE LOWER CATARRHINES (*CERCOPITHECIDAE*)
(JOHNS HOPKINS ANATOMICAL COLLECTION)

The facial musculature of the macaque has not quite evolved to the level which the higher platyrrhines have reached. This becomes evident from the fact that the postauriculo-occipital muscle group still largely arises from the nuchal region, where it has retained its primitive relations with the persisting nuchal portion of the platysma (figs. *a* and *b*). The *M. auricularis posterior*, represented by a deeper layer of the postauriculo-occipital muscle complex, has however definitely shifted its origin to the occiput (fig. *b*). In regard to the postauriculo-occipital muscle group the macaque thus exhibits conditions which can easily be derived from the plan characteristic of the lower platyrrhines. The platysma, on the other hand, shows in the macaque modifications which are undoubtedly correlated with the acquisition of the buccal pouch. This pouch is formed by a continuation of the mucous membrane of the cheek wall, lined with a strong muscular coat derived from the *M. buccinator*. It has herniated through the platysma, splitting this muscle plate into an upper and a lower portion (fig. *a*). The buccal pouch now rests upon the lower portion of the platysma subjacent to the skin (figs. *a* and *c*). Anteriorly to the buccal pouch strong crossing bundles of the platysma from the right and left side interlace (fig. *a*). This solid interlacing of platysma bundles below the chin is, no doubt, likewise correlated with the formation of the buccal pouch. Owing to the strengthening muscle coat the buccal pouch can be greatly distended. The temporarily stored food is repelled into the buccal cavity by voluntary contraction of the musculature of the pouch. However, when the pouch has been tightly packed with food and overdistended, the muscle coat of

area of overlap in periosteal sensibility. Since the *M. frontalis*, *M. occipitalis* and the superficial temporal musculature are invariably separated by considerable muscle-free areas over the vertex, periosteal and deep skin pressure could be tested best in the region of the galea aponeurotica, into which the epicranial facial muscles insert.

Besides the superficial skin sensibility, and the three-fold deep sensibility (deep skin pressure, muscle pressure and periosteal pressure) we have to consider the muscle sense (postural sense) in the mimetic musculature. This question likewise remained an open one.

Long ago Charles Bell and Magendie reported that some flattening and other changes in the contour of the face occur after section of the peripheral branches of the *N. trigeminus*. Later Krause (1895, '96), Cushing (1904) and other surgeons observed that following section of the *N. trigeminus* or of its sensory root, or extirpation of the Gasserian ganglion, certain postural deformities in the mimetic musculature may occur. Cushing was the first to ascertain the absence or presence of postural sense in cases of trigeminus section, by the use of the faradic current. According to Cushing's statements his patients were unable to appreciate muscle contraction in the mimetic musculature produced through electric stimulation,

unless the twitchings were conveyed to an esthetic area. These observations made plausible the postulate that postural sense from the mimetic musculature is transmitted through the *N. trigeminus*.

Mills (1910), on the other hand, argued that facial movements, while of much importance in expression, nasal respiration, articulation, and a few other well known functions, are probably not to any large degree dependent for their proper performance upon postural sense. The postural sense might, according to Mills, have considerable representation in an afferent system passing with the motor *N. trigeminus*. Nevertheless Mills admitted the probability that there is some postural sense conducted with the facial movements, although this may not be of much importance. Though in his stimulation experiments some observations indeed suggest transmission of muscle sense from the mimetic musculature through the *N. facialis*, Mills states that he was not able fully to convince himself that this sense of contraction was not a result of extrapolar diffusion of very strong current to neighboring areas which were esthetic, or only partly anesthetic. Thus Mills finally came to accept Cushing's conception, which evidently became the prevailing view among the neurologists (compare Kappers, 1920, p. 535).

In view of the uncertain state of the

the pouch is not sufficiently strong to expel the food. Under such circumstances the animal pokes the food back into the buccal cavity with the aid of the fist. The other representatives of the Cercopithecinae show similar conditions, while the representatives of the Semnopithecinae, the second family of the Cercopithecidae, lack a buccal pouch.

In regard to the *Sphincter colli profundus* and its derivatives, the lower Catarrhines have evolved above the level of the lower platyrrhines. As in the higher platyrrhines, the *sphincter colli profundus* layer has been dropped from the plan of facial musculature, and vestiges of it are only occasionally encountered as individual variations. This holds true for the entire catarrhine branch. The derivatives of the *Sphincter colli profundus* are well developed though not greatly differentiated in the lower catarrhines: The *M. auricularis anterior et superior*, the orbito-auricular musculature, and the *M. frontalis* still form a primitive muscle complex which covers the anterior part of the calvarium (figs. *a* and *c*). Little differentiation has likewise taken place in the musculature of the midface region. There, the powerful zygomaticus muscle mass remained in broad connection with the *M. orbicularis oculi*, and the *M. naso-labialis* forms a continuous muscle plate which covers the whole nose and expands lateralward into the upper lip (fig. *c*). Lateral to the angle of the mouth appears the *M. triangularis* (figs. *a* and *c*), characteristically overlapping the platysma. It has however not yet expanded as far as the lower border of the mandible, as in the higher catarrhines.

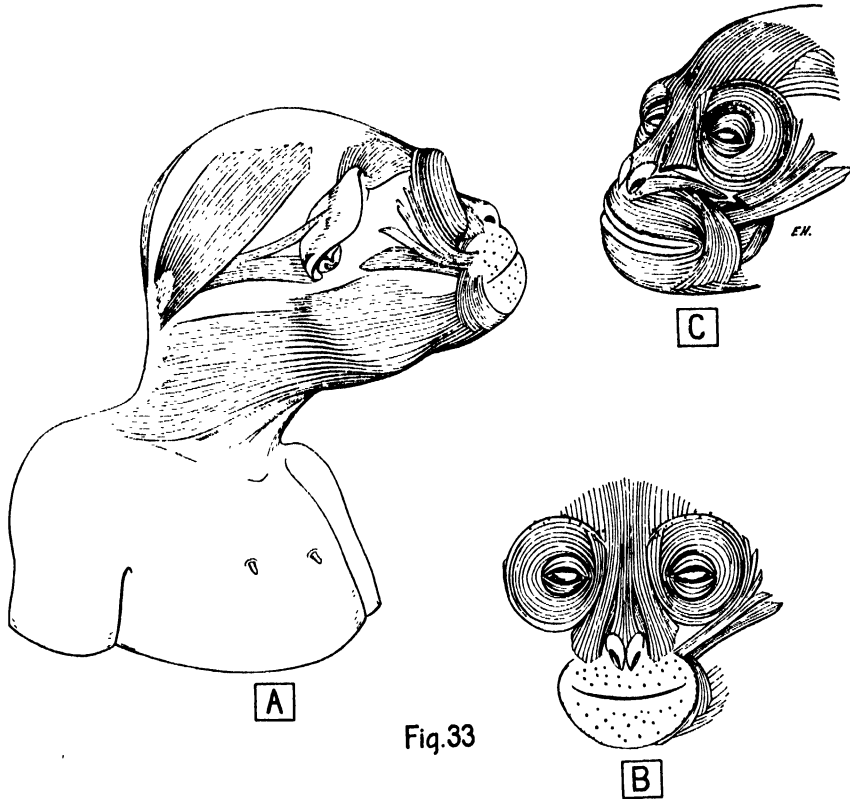


Fig.33

FIG. 33. HYLOBATES PILEATUS (GIBBON) (JOHNS HOPKINS ANATOMICAL COLLECTION)

In their plan of the superficial facial musculature the gibbons show conditions in various regards intermediate between the lower catarrhines and the great anthropoid apes and man. This is clearly seen in the arrangement of the postauriculo-occipital musculature and its relation to the deteriorating nuchal portion of the platysma. The muscles of the face proper, the derivatives of the *sphincter colli profundus*, show primitive conditions combined with strikingly progressive features, which lift the gibbons above the lower catarrhines: the *M. frontalis* is partly set off from the orbito-auricular muscle complex (figs. *a* and *c*). Noteworthy is the indication of a separation of the *M. nasolabialis* into three portions, i.e. two bilateral *Mm. levatores labii superiores*, and a middle unpaired portion, which extends from the glabella downward over the entire back of the nose to be inserted below into the alae nasi (fig. *b*). This middle portion evidently corresponds to the musculature which in man gave rise to the *M. procerus nasi sive depressor glabellae* and to the very variable, inconstant vestiges represented by the *Mm. dilatores narium ant. et post.* and the *M. apicis nasi*. Between the three portions just described there are more feeble intermediate muscle bundles. Note that in the glabellar region the three portions remain as one, having preserved the broad connection with the *M. frontalis*. This broad secondary fusion of portions of the supraorbital and infraorbital muscle complexes occurs in the lower primates (compare fig. 29*d*, 30*d*, etc.). It persists throughout the "ascending scale of primates" up to man (compare Huber, 1926/27).

The *M. triangularis* in the gibbon has extended further downward when compared with conditions found in the lower catarrhines. It reaches the lower border of the mandible. The orbicularis-buccinator group (partly shown in fig. *c*), although more highly evolved than in the lower catarrhines, has not attained the complexity of the corresponding muscle group of the great anthropoid apes and man. Strangely primitive among the derivatives of the *pars oris, sph. colli. prof.*, is the *M. maxillo-naso-labialis* (fig. *c*), which has hardly evolved above the stage of the primitive simian plan, while the same cannot be said of the lower catarrhines.

Hylobates (gibbon) and *Symphalangus* (siamang), the two genera of the Hylobatidae, show a very similar arrangement of the superficial facial musculature. In some regards, however, *Symphalangus* stands a little higher than *Hylobates* (compare Ruge, 1911).

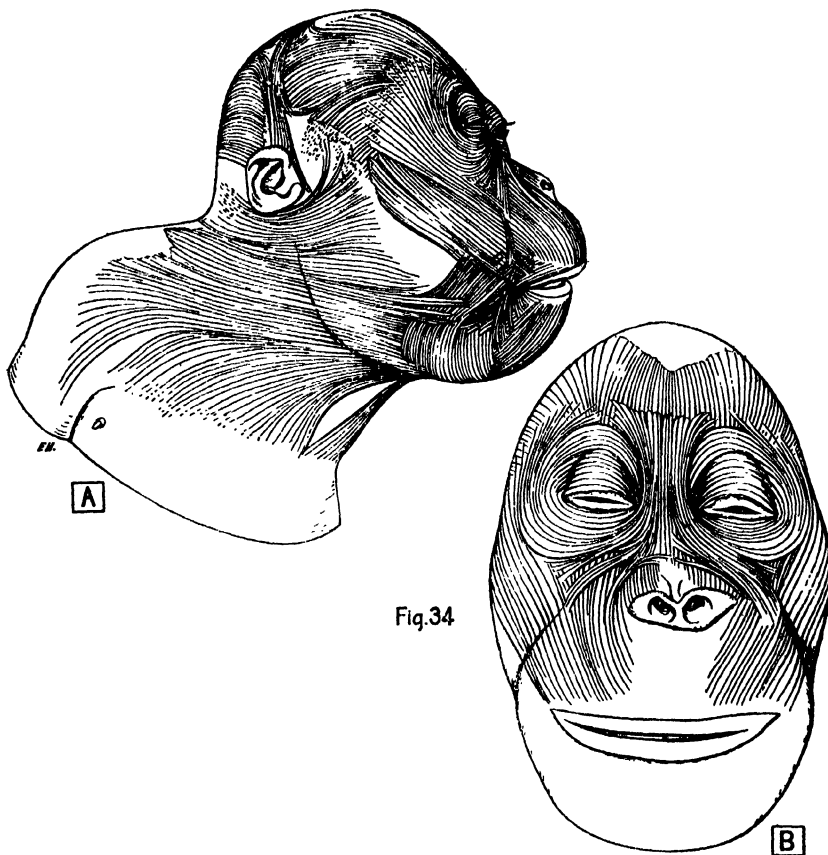


Fig. 34

FIG. 34. HALF GROWN ♂ ORANG (PONGO) (JOHNS HOPKINS ANATOMICAL COLLECTION)

The plan of the superficial facial musculature of the orang shows striking deviations from the ground plan of the other two great anthropoid apes (chimpanzee and gorilla) and man. The platysma is peculiar through its bony attachment with a slip to the acromion (fig. a). The postauriculo-occipital muscle group covers the occiput like a little cap; it sends a muscle slip to the auricle, and there is an additional, deep *M. occipitalis* (not shown in figure). The most peculiarly shaped *M. auricularis superior* ascends as a rather narrow band as far as the height of the vertex, while a small slip of it has extended a short distance downward in front of the ear. This *M. auricularis superior* belongs entirely to the postauricular muscle group, as shown by its nerve supply (Huber, in disagreement with Ruge and Popowsky), while, on the other hand, the *M. auricularis ant. et sup.* of chimpanzee, gorilla and man represents a fusion of a postauricular with a preauricular portion. The *Mm. auriculares proprii* of the orang, which have received little attention by previous investigators with the exception of Ruge, are further deteriorated than those of the chimpanzee, gorilla and man. Traces of all of them were, however, detected in the specimen investigated by the author, in contrast to the specimen of Ruge.

Among the derivatives of the *Sphincter colli profundus* (figs. a and b) the well developed, but not further subdivided orbito-auriculo-frontal muscle complex covers the anterior half of the calvarium (fig. a). The preauricular portion is reduced to a tendinous plate, which does not reach the ear,—this in striking contrast to the chimpanzee, gorilla and man. The zygomatico-orbital muscle plate of the orang is without attachment to the zygomatic arch. It is still in broad connection with the *M. orbicularis oculi*. The *M. triangularis* is very powerfully developed, and differs in proportions from that of the chimpanzee, gorilla and man. In the glabellar region (fig. b) the muscle corresponding to the *M. procerus nasi sive depressor glabellae*, is inserted above with superficial muscle bundles into the subcutaneous tissue; with its deep bundles, however, it remains continuous with the *M. frontalis*.

The orbicularis oris-buccinator group (not shown in figures) is far more complex than in the gibbons and the lower catarrhines; but it differs fundamentally in its architecture from the similarly complex musculature of the chimpanzee, gorilla and man.

The findings of previous investigators (Ruge, Popowsky, Sullivan and Osgood, Lightoller) give evidence that the features here emphasized as striking peculiarities of the orang, are not mere individual variations but really belong to the ground plan of this animal.

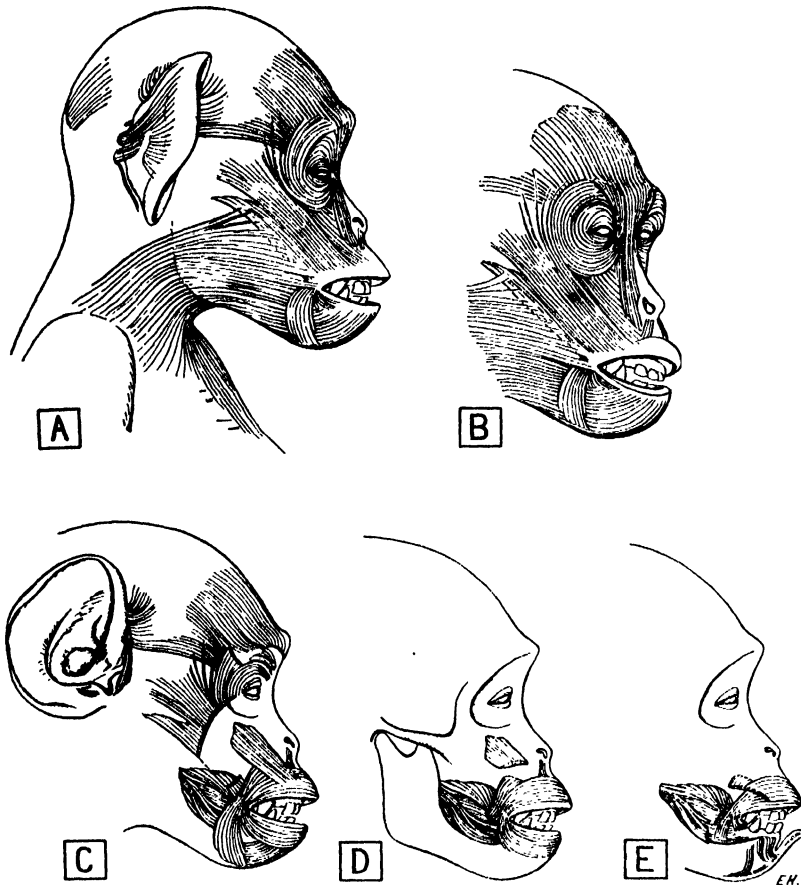


Fig. 35

FIG. 35. YOUNG ♂ CHIMPANZEE (*PAN*) (COLLECTION OF THE DIVISION OF MAMMALS, U. S. NATIONAL MUSEUM)

The plan of the superficial facial musculature of the chimpanzee closely corresponds with that of the gorilla (fig. 36). Both chimpanzee and gorilla share with man, not only a common ground plan but also similarly directed evolutionary trends: there exists on one hand, a striking tendency towards reduction of the superficial muscles of the temporal and occipital regions and structural as well as functional deterioration of the entire ear musculature (figs. *a* and *c*), while the musculature of the face proper tends towards fuller development and further differentiation. However, as to structural differentiation, but especially in regard to functional perfection of the musculature of the face, man excels by far the great anthropoid apes (orang, chimpanzee and gorilla).

In figure *c* the formation of a *M. corrugator supercilii* with firm origin from the frontal bone is noteworthy. This formation is characteristic of chimpanzee, gorilla and man. A corresponding deep muscle portion, though not detached from the *M. frontalis*, exists also in the orang, while the gibbons and lower catarrhines lack such a differentiation. Common to all, however, is the *M. depressor supercilii*, which has been retained from the primitive primate ground plan. This is the muscle which in the lower primates controls the supraorbital tactile vibrissae (compare figs. 28, 29, 30 and 31*a* and *b*).

Figs. 35*c-e* show the derivatives of the *pars oris ssp. colli profundus*. This musculature has reached a high complexity which cannot be brought out fully in this short discussion and with only a few figures (compare further Virchow, 1915). A comparison of figure 35*c* with figure 33*c* of the gibbon shows that the *M. maxillo-labialis* in the chimpanzee has shifted its origin higher up on the maxilla. Through this it became a *M. levator labii superioris proprius*. This is characteristic not only of the three great anthropoid apes and man, but also of the lower catarrhines; while the gibbons, as already pointed out, have retained more primitive conditions. The *M. nasalis* of the chimpanzee (figs. *a-d*) shows a similar arrangement to that in gorilla and orang, in contrast with conditions found in man. The *M. mentalis* (fig. *e*) is seen in close, primitive relation to the *M. buccinator* (Huber), while a deep bundle of the platysma inserts in the immediate neighborhood, a finding which misled Ruge to derive the *M. mentalis* from the platysma.

question, and considering the fact that efforts to demonstrate muscle spindles in the mimetic muscles had been without success, the author found it worth while to submit himself to a somewhat painful procedure. In collaboration with Walter Hughson, a surgeon, the following experiments were undertaken: With the unipolar electrode there were determined in the author's face the sites of the individual facial branches from which a definite response of the mimetic muscles over the forehead, in the supraorbital and glabellar regions, and on the cheeks could be obtained. These spots were then marked with indelible ink. Keen appreciation of contraction of the responsive mimetic musculature facilitated this preliminary test.

In order to determine now whether the contraction of the electrically excited mimetic muscles was indirectly appreciated through the pathway of the cutaneous branches of the *N. trigeminus* over the areas under observation, the *rami frontalis* and *supraorbitalis*, and the *N. infraorbitalis trigemini* were blocked with novocain. After complete anesthesia of the respective areas, the previously mapped out individual facial branches were alternately stimulated as in the preliminary test. And in every instance the author with closed eyes was able not only to tell, without delay, when muscle groups or muscle portions under stimulation were contracting, but also to name the individual facial branches which must have been electrically stimulated in order to bring about the appreciated contraction of the respective muscle group or muscle portion.

These experiments give ample evidence that we have indeed in the mimetic musculature muscle sense, which is conducted together with the muscle pressure sensibility, by the muscle branches of the *N. facialis*. It is likely that under normal

circumstances, in addition to the direct appreciation of muscle contraction with the aid of muscle sense (*N. facialis*), postural sensations are carried back through the *N. trigeminus* from the skin when the latter is under tension and wrinkled through the contracting mimetic muscles.

It remains for future investigations to detect in the superficial facialis musculature the sensory organs which correspond to the muscle spindles of the rest of the voluntary musculature. More recent investigations along this line by Olive C. Smith, with the methylene blue technique, have so far been negative (compare Hines, 1927, p. 159, 167).

IX. REFLEX CONNECTIONS BETWEEN THE SENSORY TRIGEMINUS FIELD AND THE FACIAL MUSCULATURE. ANASTOMOSES OF THE *N. FACIALIS* WITH OTHER NERVES

Lastly, brief consideration will be given to the functional connections between the sensory field of the *N. trigeminus* (skin, conjunctiva of the eyes, mucous membranes of nose, lips and buccal cavity) and the facial musculature. With the expansion of the superficial facial musculature over the entire face in mammals (chapter I) and the simultaneous evolution of the sensory field of the *N. trigeminus* (chapters IV, V, VI), functional connections were established between the two fields, which do not exist in vertebrates below the mammals. Those subdivisions of the motor facial nucleus which represent the primary motor centers for the superficial facial musculature (ear muscles, muscles of the face: vibrissae moving muscles, muscles of the snout, lips and cheek wall, and above all the *M. orbicularis oculi*, the protecting muscle of the eye) were brought under the influence of the sensory trigeminus. Thus new arcs were established for reflexes, among them such vitally important ones as the suckling

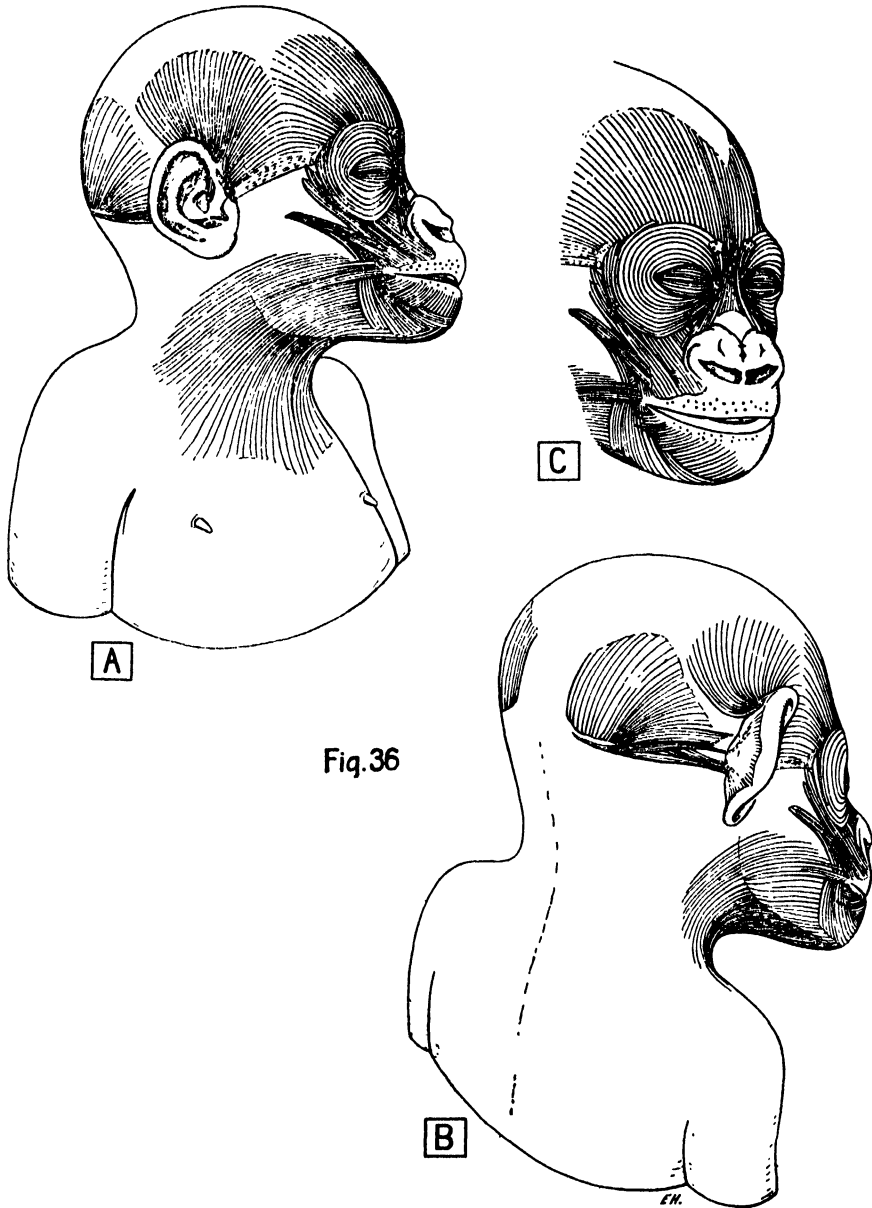


Fig. 36

FIG. 36. YOUNG ♀ GORILLA (*G. GORILLA*) (COLLECTION OF DEPARTMENT OF COMPARATIVE ANATOMY, AMERICAN MUSEUM OF NATURAL HISTORY, NEW YORK)

The figures show the superficial facial musculature on a plan which is characteristic of the gorilla, chimpanzee and man. Through the loss of the nuchal portion of the platysma the postauriculo-occipital muscle group has become completely isolated in the occipital region (figs. *a* and *b*). The *M. occipitalis* (fig. *b*) arises from the linea nuchae superior. There is a considerable space between the occipital musculature of the two sides. The *M. auricularis posterior*, still in close relation with the *M. occipitalis*, is represented by several slips which insert into the ear cartilage. The muscle is at the origin reduced to a tendinous band. This gives evidence that the evolutionary tendency of the extrinsic postauricular musculature is to shift closer to the ear. The same trend is clearly seen also in the chimpanzee (fig. 35*a*) and man (compare succeeding figures). The range of in-

reflex, and the ocular reflex. In connection with the latter it may be stated that the effective reflex closure of the eyelids with the aid of the *M. orbicularis oculi* rendered more or less superfluous the nictitating membrane, a phylogenetically older eye protecting structure, which in certain mammals, including the Primates, has become reduced to a mere vestige.

Throughout the orders of mammals some of the muscle branches of the *N. facialis* anastomose with branches of the *N. trigeminus* as well as with branches of the cervical plexus. This fact has led a series of previous authors (Leche, Westling, McKay, Kohlbrugge, v. Bardeleben, Eisler, Edgeworth, Poirier and Charpy, *et alii*) to assume that through such anastomoses the superficial facial musculature

receives an additional motor supply. Although such an assumption could be discounted on the basis of comparative anatomical and embryological investigations, which had afforded convincing evidence that the superficial facial musculature represents a genetic entity, a muscle territory under the exclusive domain of the *N. facialis* (chapter I), it was important to give supplementary proofs of it to those who were sceptical of data from comparative anatomical and embryological investigations. It is impossible to untangle by purely morphological methods of investigation the complex anastomoses of the *N. facialis* with the branches of the *N. trigeminus* and with nerves of the cervical plexus. Here, the experimental method alone could bring a satisfactory solution.

dividual variations with transitions from primitive to more progressive conditions is very considerable in all three types. Moreover, there is a conspicuous tendency towards deterioration of this muscle group. It may be added that ear movements in the gorilla and chimpanzee have been noted to be almost as rare as in man. In the case of the chimpanzee shown in figure 35*a*, contrasted with the gorilla of figure 36*b*, the postauriculo-occipital musculature has reached an extreme degree of regression, the *M. auricularis posterior* being represented in this case by short muscle slips which have settled down very close to the ear, while the much reduced vestigial *M. occipitalis* remained isolated in its original position. There have been cases reported where the *M. occipitalis* of the chimpanzee was completely deteriorated.

The orbito-auricular muscle complex of the gorilla (fig. 36*a*), although still with primitive extension in this specimen (compare case of Ruge, 1887*a*), is in part reduced to a tendinous plate, intermediate between the *M. frontalis* and the *M. auricularis ant. et sup.*

Among the muscles of the face proper (figs. 36*a* and *c*) conditions of the zygomatico-orbital muscle mass are noteworthy. While this muscle mass has retained a broad connection with the *M. orbicularis oculi*, the lateral portion of it, which in the chimpanzee (fig. 35*a*) has settled down on the zygomatic arch, is in the gorilla clearly set off as a well defined "*M. zygomaticus*". This was found also in other specimens of gorilla dissected by previous authors (compare e.g., Ruge, 1887*a*). That the *M. zygomaticus* of the gorilla, however, should not be considered fully homologous with the human zygomaticus muscle, becomes evident from a comparison with primitive and progressive stages of zygomaticus formations in man. While in the White race the *M. zygomaticus* in a prevailing percentage of cases is a distinct muscle with bony origin from the zygoma, in other races as a rule only deep bundles of the zygomatico-orbital muscle mass have settled down on the zygomatic arch, while the bulk of superficial bundles are anchored in the subcutaneous tissue of this region, often extending further back in the direction of the ear. The well defined *M. zygomaticus* of the White may be derived from such a more primitive arrangement through loss of the superficial zygomatico-orbital bundle mass and persistence of the deep muscle portion attached to the zygoma. Various intermediate stages illustrating such a transformation are found as individual variations in the White.

The *M. triangularis* in gorilla and chimpanzee is of similar proportions to that of man; it is fixed with its base to the platysma, but has not yet become attached to the mandible, as in the latter.

In both gorilla and chimpanzee, as well as in occasional cases of man a group of platysma bundles cross the *M. triangularis* at the junction of this muscle with the *M. caninus* to become inserted into the angle of the mouth. This muscle portion, often referred to as *M. risorius*, is not a real *Risorius*. The true *M. risorius Santorini*, usually composed of deviating marginal bundles of the *M. triangularis*, is peculiar to man. That deviating bundles of the *M. zygomaticus*, or of the platysma, or of both, may join or even replace the true *M. risorius Santorini*, is well known to those who have studied this extremely variable formation in a larger series of human bodies.

The nasal musculature shows differences in the gorilla, chimpanzee and man, according to the conspicuous differences in the formation of the nose of the three types. In man this musculature is more highly evolved and developed on a somewhat different plan than in the gorilla and chimpanzee, which show greater resemblance to one another. Their plan of nasal musculature is similar to that of the orang.

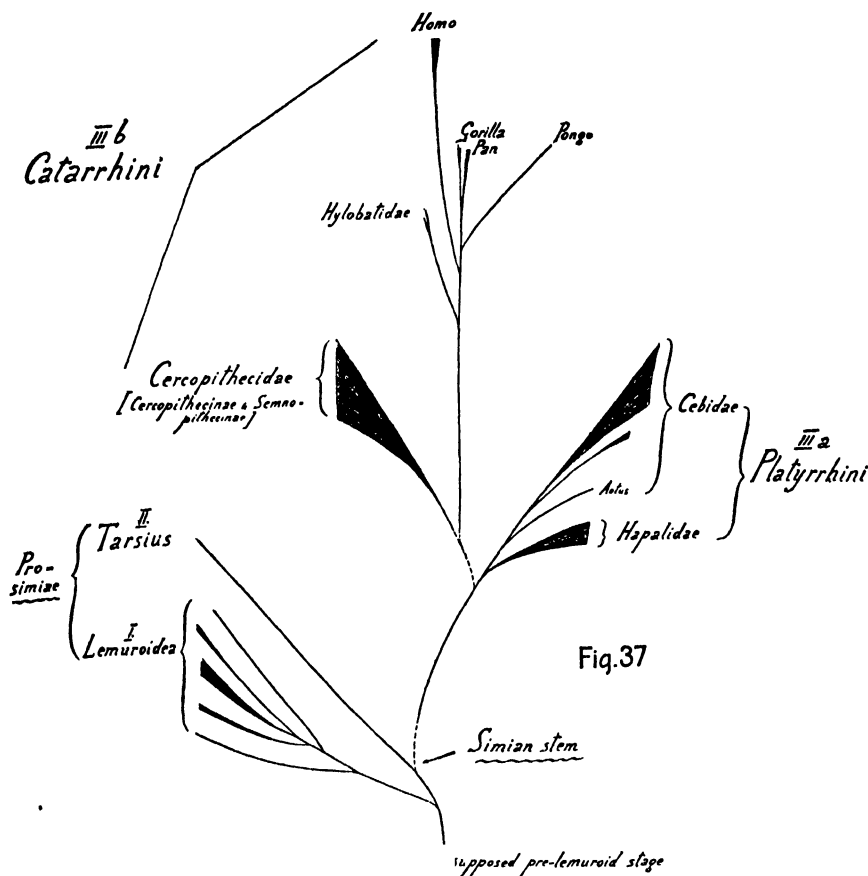


FIG. 37. SCHEME REPRESENTING THE AUTHOR'S CONCEPTION OF THE PROBABLE GENETIC RELATIONSHIP OF THE LIVING PRIMATES, BASED ON INVESTIGATION ON THE FACIAL MUSCULATURE (No consideration is given to the time element, nor are the adaptations to different habitats taken into account)

Lemuroidea and Tarsoidea are shown as divergent branches of a common prosimian stock. The separate lines of the lemuroid branch represent the existing divergent lemuroid types, which are to be considered more closely related to each other, in contrast to the independent branch leading up to modern *Tarsius*.

The Simian stem is derived from an early, generalized tarsioid form, which first gave rise to primitive platyrrhine monkeys. From these early platyrrhine forms evolved the various groups of the modern platyrrhines, while one type, it is thought, gave rise to the catarrhines. The indicated subdivision of the platyrrhines into only two families, the Hapalidae and the Cebidae, should not be considered final: While the various genera of the Hapalidae form a natural group, there are various primitive intermediate types (e.g. *Aotus*) included within the Cebidae, which may possibly represent distinct families.

The catarrhine branch is shown splitting up early into the Cercopithecidae and the higher catarrhines. Within the family of the Cercopithecidae no further consideration is given to the genetic relationship of the subfamilies of the Cercopithecinae and Semnopithecinae and their genera. The genetic relation of the members of the anthropoid-human branch is further considered in the next figure.

A recent study by Michelsson (1921), and more extensive investigations by the author in collaboration with Hughson (electrical stimulation of the first five cervical nerves, the *N. trigeminus* and the

N. facialis, and cutting of the peripheral branches of the *N. facialis* with consequent loss of function and degeneration of the corresponding facial muscles) have given conclusive evidence that the anastomosing

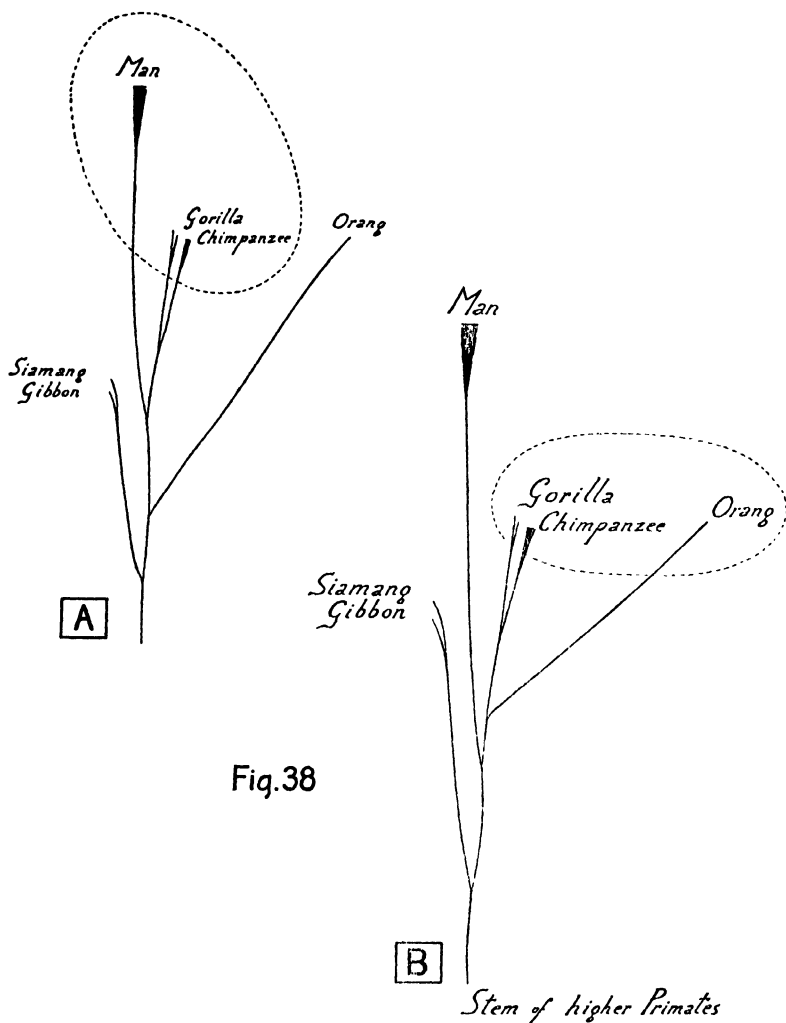


Fig.38

FIG. 38. SCHEME REPRESENTING THE AUTHOR'S CONCEPT OF THE GENETIC RELATIONSHIP OF THE LIVING HIGHER PRIMATES

The gibbons, having undoubtedly early branched off from the common anthropoid-human stem, have, except for the extreme specializations in connection with their brachiating habits, preserved a more primitive ground plan compared with the great anthropoid apes. In a series of features they are intermediate between the lower catarrhines, on one side, and the great anthropoid apes and man on the other. While thus, judged by the findings on the facial musculature as well as on other organ systems, there can be little doubt about the position of the gibbons, the genetic relations between the orang, and the chimpanzee and gorilla, and the relation of man to the great anthropoid apes appear more problematic. From the fact that the orang, in regard to facial musculature and other organ systems, differs so widely from the chimpanzee and gorilla, while the latter two share with man a common ground plan of facial musculature and strikingly similar evolutionary tendencies within this muscle field, one may be tempted to derive man directly from the line leading up to the chimpanzee and gorilla and to separate, on the other hand, the orang from the chimpanzee and gorilla, as indicated in fig. 38a. However, giving weight to the likeness of the three great anthropoid apes in many features of the various organ systems, and considering their likeness in general appearance and psychology, one can hardly separate them. It therefore seems more reasonable to derive man from the anthropoid-human stem before the three great anthropoid apes had evolved from this stem, as indicated in fig. 38b. According to this second scheme the orang would, after an early departure from the great anthropoid stem, have sidetracked with high evolutionary trends of his own, while chimpanzee and gorilla evidently stayed closely together. And parallel to them developed man with evolutionary trends innate to all three.

Although the author in the text conservatively referred to the various races of man, it would seem to him justifiable to value these "races" as distinct species, thus applying the same measure as generally applied in evaluating the various types of chimpanzees and gorillas.

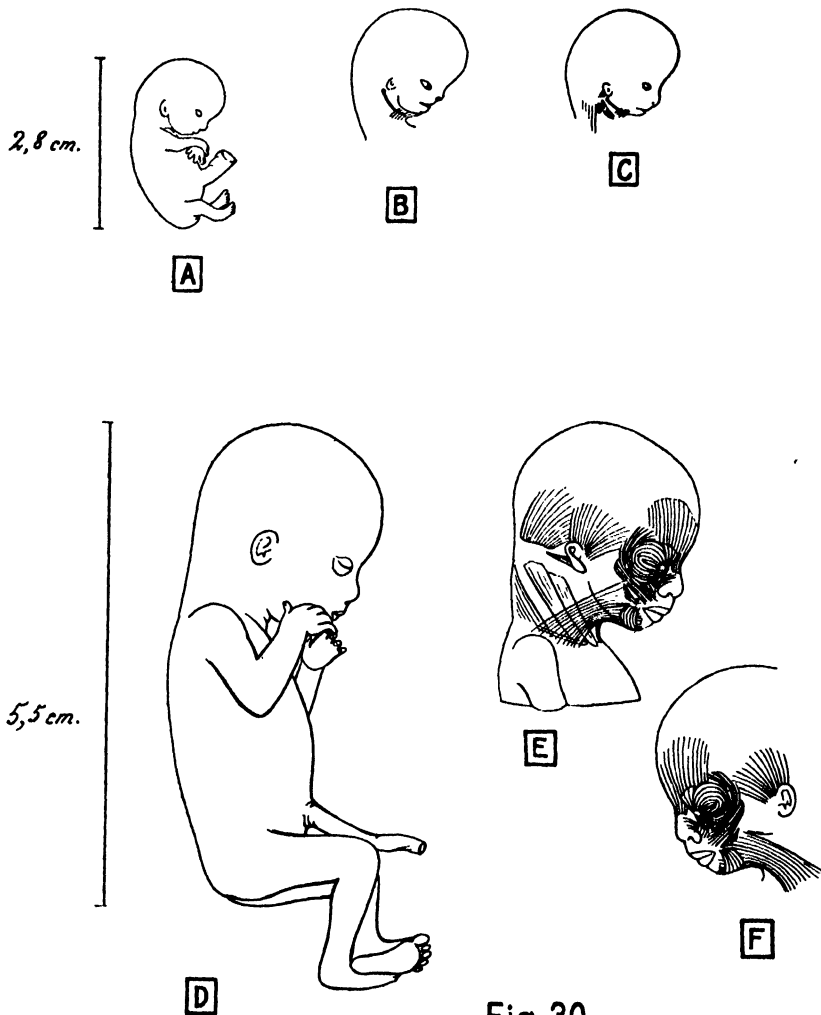


Fig. 39

FIG. 39. EARLY STAGES IN THE EMBRYOLOGICAL DEVELOPMENT OF THE MIMETIC MUSCULATURE OF MAN

A and C. Human embryo of the end of the 2nd month, 2.8 cm. crown-rump length (No. 1460 of the Collection of the Carnegie Laboratory of Embryology, Baltimore).

B. The same stage, after Popowsky (1895): anlage of the platysma with its innervation through the N. facialis. According to Popowsky there are in this stage no mimetic muscles besides the neck portion of the platysma. However, the author could, in his specimen (compare fig. c) with the aid of the dissecting microscope demonstrate the presence of the *M. auricularis posterior*. This muscle was even further advanced in development than the barely recognizable platysma. It showed a close, primitive relation to the *M. biventer posterior* of the deep facial muscle group, which was still further advanced in its differentiation, about to the degree of the well defined anlagen of the sterno-cleido-mastoideus and trapezius muscles. Microscopic studies by Zuckermann-Zicha (1925) moreover give evidence that around this stage the first histological differentiation of muscles in the face (*M. orbicularis oculi*) take place. It is interesting to see that during the embryological development certain groups of the facial musculature precede in their differentiation other groups. The critical period of development and differentiation of the mimetic musculature is evidently between the 2nd and 3rd month of fetal life, as seen from the following figures.

D—F. White male fetus of the end of the 3rd month, 5.5 cm. sitting height (No. 4808 of the Collection of the Carnegie Laboratory of Embryology).

branches in question, of the *N. trigeminus* and cervical nerves with the *N. facialis*, are not motor (compare Huber, 1924; Huber and Hughson, '26).

Renewed claims by Edgeworth (1928) that the platysma in the opossum is innervated by additional branches from the cervical plexus, have lately been disproven through experiments repeated by W. K. Smith (unpublished).

The question now arises, what significance the anastomoses under consideration do have, motor function to the facial musculature having been definitely excluded. The author has hitherto been inclined to consider these anastomoses as mere topographic relations. It was thought that certain sensory branches of the *N. trigeminus* and nerves of the cervical plexus ramifying in the same areas where the muscle branches of the *N. facialis* ramify, came in some places to lie so close together with the latter that they were subsequently bound together by common connective tissue sheathes. After a joint journey, it was assumed, the sensory branches of the trigeminal and cervical nerves would separate again from the muscle branches of the *N. facialis*, the various nerve elements finding thereafter

the tissue which they were destined to supply (Huber, 1922-23, p. 384-386). This concept is, however, open to criticism until adequate experimental data are available, which definitely exclude functional relations. There is a possibility that by the way of the anastomoses of these cutaneous branches of the *N. trigeminus* and cervical nerves to the muscle branches of the *N. facialis*, the blood vessels within the superficial facial musculature receive their vaso-motor supply.

SUMMARY AND CONCLUSIONS

In this paper comparative anatomical, racial anatomical and embryological studies on the *facialis* musculature, and studies on the cutaneous field of the *N. trigeminus* are correlated with the data obtained from neuro-physiological investigations.

Although in lower vertebrates up to the Sauropsida the *facialis musculature* is but of moderate extension, it has in mammals attained a unique development. After having become completely separated from the deep *facialis* musculature, the superficial *facialis* musculature expanded over the whole head and face.

The Monotremes developed the super-

This fetus had been recovered from a miscarriage, and under special care survived for half an hour. The author thus had an opportunity to stimulate with the unipolar method the various branches of the *N. facialis*. The mimetic muscles responded by definite contraction to the electrical stimuli of the corresponding muscle branches. Fine wrinkling of the delicate skin in the various regions of the face, and movements of the ears were clearly noticeable. This experiment thus revealed the fact that the motor nerves are capable of carrying electrical impulses to the muscles at an earlier stage than previously demonstrated by Minchowski (1928), who found the peripheral nerves responsive from the fourth month on. The experiment moreover gave evidence that, contrary to the statements of Popowsky (1895), the mimetic musculature at the end of the 3rd month is already regionally differentiated. This was subsequently corroborated by detailed, careful dissection of the fetus, which had been preserved in Bouin's fluid. The findings are illustrated in figs. 39*e* and *f*. Note, by careful comparison of the right and left aspect represented in these two figures, that already at this early stage variations on the right and left sides are recognizable. These asymmetries become more marked in the following stages, as the structures receive more elaborate differentiation. While the fixation in Bouin's fluid proved very satisfactory for detailed dissection under the binocular lens and dissecting microscope, it was impossible to see in this fetus the characteristic gelatinous, half transparent consistence of the mimetic muscles, or to demonstrate the various phases of differentiation in which the given muscle groups appear at this stage. These characteristics, however, were clearly noted in a formalin preserved specimen of the same stage dissected by the author side by side with the one preserved in Bouin's fluid.

Preliminary parallel investigations, which the author has carried out on embryo and fetal pigs, suggest that on account of the different rate of differentiation of the various muscle groups the study of the embryological development of the muscle system may eventually prove very helpful in correlating the corresponding developmental stages in the mammalian series up to man.

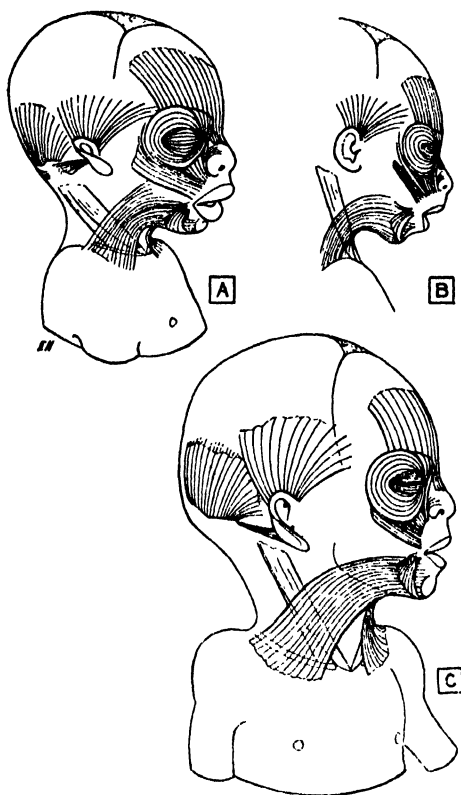


Fig. 40

FIG. 40. FURTHER DEVELOPMENT OF THE MIMETIC MUSCULATURE AND RACIAL DIFFERENTIATION IN NEGRO AND WHITE FETUSES OF THE 4TH AND 5TH MONTH

Male Negro fetus (A) of the end of the 4th month (No. 1524, 13.2 cm. sitting height) compared with male White fetus (B) of the end of the 4th month (No. 3047, 12.8 cm. sitting height) and male White fetus (C) of the 5th month (No. 4914, 17.9 cm. sitting height), all three of the collection of the Carnegie Laboratory of Embryology.

Racial differences show up as early as the 4th month, where the mimetic musculature of the Negro (A) is more coarsely bundled, and the individual muscles appear more compact when compared with those in the White (B). Conspicuous is the heavy zygomatic muscle mass which is directly continuous with the *M. orbicularis oculi*. Contrasting strikingly with the Negro the author found in the 4 month White fetus (B) a well defined *M. zygomaticus*, which had settled down on the zygomatic arch and which at its origin was completely separated from the muscle portion intermediate between the *M. zygomaticus* and the *M. orbicularis oculi*. The entire mimetic musculature in this White fetus was more delicately bundled, and the individual muscles were of a more gracile type.

Again in the 5 month White fetus (C) the *M. zygomaticus* was represented by a well-defined muscle which was completely set off from the *M. orbicularis oculi*, although the marginal bundles of the latter overlapped the *M. zygomaticus* at its origin. In addition, there was present a well defined caput zygomaticum of the *M. quadratus labii superioris*.

In general it may be stated that in both Negro and White up to the end of the 5th month the mimetic musculature is of gelatinous, half transparent consistence while the subjacent skeletal muscles are considerably further developed and more compact. This is indicated in all three figures, where the *M. sterno-cleido-mastoides* and the clavicle are seen shining through the delicate platysma plate.

facial facialis musculature along their own different from the common marsupio-
line, on a ground plan which is distinctly placentalian ground plan. Notable dif-

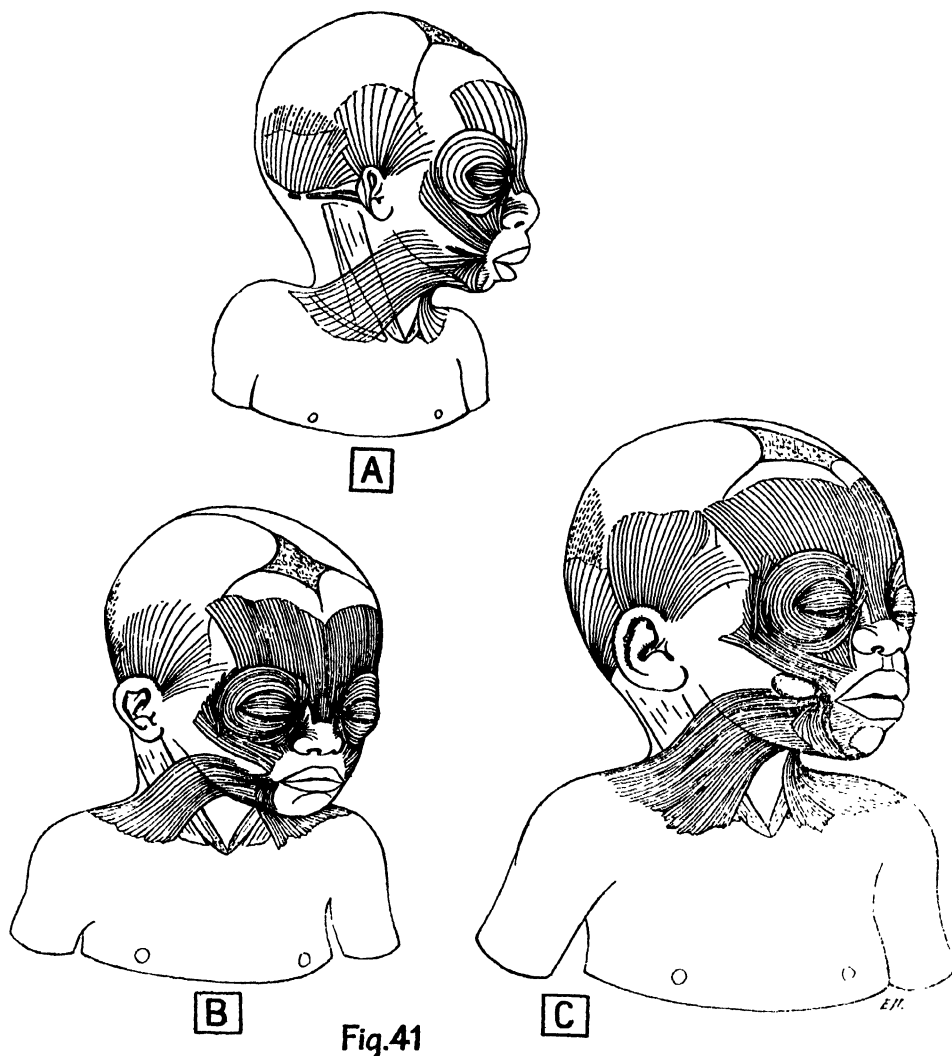


Fig.41

FIG. 41. SUBSEQUENT STAGES OF DEVELOPMENT OF THE MIMETIC MUSCULATURE IN 3 MALE NEGRO FETUSES OF 4½, 6 AND 7 MONTHS (A. No. 4067, 15.7 cm. sitting height; B. No. 2397, 24.3 cm. sitting height; C. No. 2590, 26.3 cm. sitting height; all three of the Collection of the Carnegie Laboratory of Embryology).

These fetuses were dissected side by side with corresponding stages of the White. Again the Negro characteristics were found well expressed: The entire mimetic musculature appeared more coarsely bundled, and the individual muscles were more compact as compared with the White. There was a lack of differentiation, especially in the musculature of the mid-face region. Note in all three that the massive *M. zygomaticus* is continuous with the muscle bundles which intermediate with the *M. orbicularis oculi*. Only the deep bundles of the zygomaticus muscle mass have gained bony attachment to the zygoma, and there is no caput zygomaticum differentiated. The large size of the *M. orbicularis oculi* is also noteworthy. The proportions of this muscle moreover differ from those of the White. It is the supraorbital portion which exceeds in width that of the infraorbital portion. In the White it is just the reverse.

While in the fetus of 4½ months the mimetic musculature was still of gelatinous, half transparent consistence—note the *M. sterno-cleido-mastoideus* and the clavicle shining through the platysma plate—there was already an indication of reddish-brown coloring to be noticed in the postauriculo-occipital musculature. The tendinous portion of the *M. occipitalis* was thus more clearly set off from the muscular portion. As mentioned before, this muscle group somewhat precedes in structural differentiation the other groups of the superficial facial musculature. In the following stages of the 6th and 7th month (figs. b and c) the entire facial musculature has lost its gelatinous, transparent appearance and is more compact. The proportions of the individual muscles also have become more like those of the new-born, which are largely like those of the adult (compare with figs. 42 and 44a).

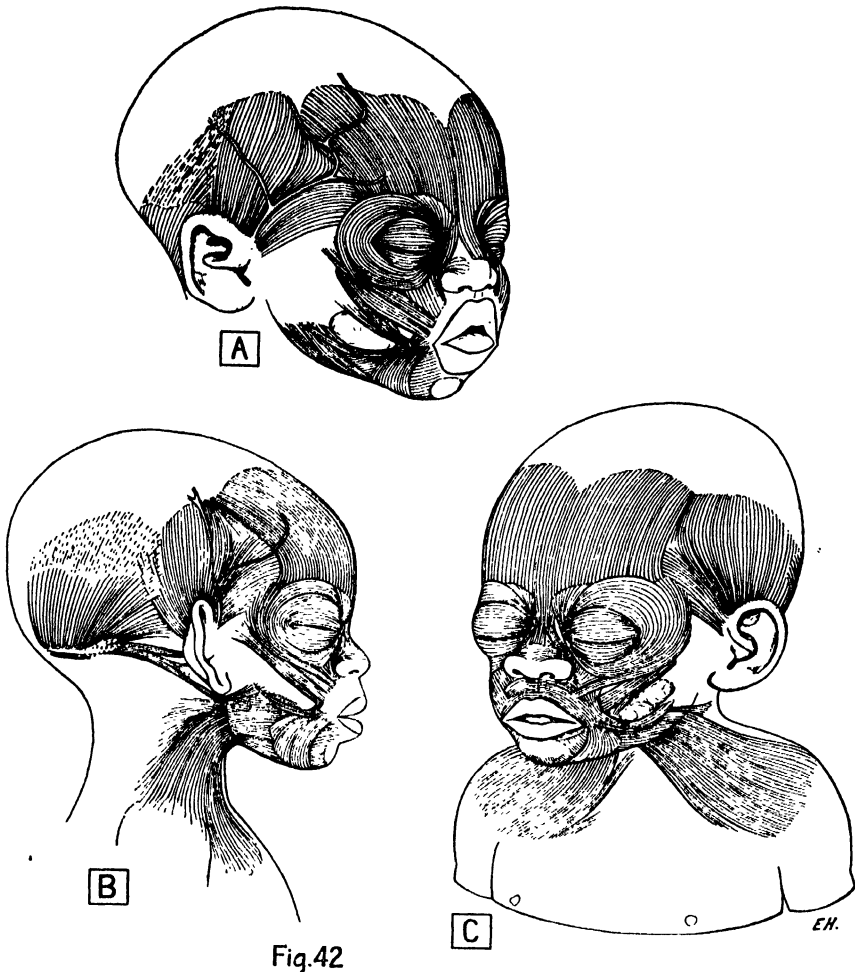


Fig.42

FIG. 42. NEW-BORN NEGROES, FEMALE (A) AND MALE (B AND C), OF THE COLLECTION OF THE CARNEGIE LABORATORY OF EMBRYOLOGY, SHOWING AS THE PRECEDING FIGURES, THE NEGRO CHARACTERISTICS, AND IN ADDITION SOME NOTABLE INDIVIDUAL VARIATIONS

Individual variations are very numerous in the superficial facial musculature. They appear early in fetal life, as seen from the previous figures, and when once laid down they naturally persist to adult life. Many of them can only be satisfactorily explained on an evolutionary basis. Note (e.g., in fig. *b*) the primitive connection between the platysma and the postauriculo-occipital muscle group. Such vestiges of the nuchal portion of the platysma are occasionally encountered in the various human races, including the White. They refer far back to our primate ancestry. A last vestige of the nuchal portion of the platysma usually isolated in the occipital region is the *M. transversus nuchae*, traces of which are, in one form or another, almost constantly found in man up to the adult stage (note this little muscle in fig. 42*b* and compare following figures). The percentage of occurrence of such vestiges is in reality much higher than usually quoted in tabulations.

The extension of the platysma further down over the upper part of the chest (fig. 42*b*) is a progressive feature in the "ascending scale of the primates." It is characteristic of the great anthropoid apes and man. In man the platysma plates of the two sides are usually far apart below (fig. 42*c*). Above, they join just below the chin, this in contrast to the findings in the great anthropoid apes. Lower crossing of the platysma plates in the regio mediana colli, occasionally encountered as individual variations, seems to be more frequent in the Negro.

In figs. 42*a-c* there may be noticed a primitive extension of the superficial musculature over the temporal region; however, the *M. frontalis* shows the tendency to become set off from this muscle complex. The zygomaticus muscle mass is undifferentiated and remains in broad primitive connection with the *M. orbicularis oculi*, as in the previous stages of the Negro. The *M. triangularis* is fixed with its base to the mandible. Derivatives of the *M. triangularis* present, are the *M. risorius Santorini* and the *M. transversus menti*.

Variation studies give evidence that the evolution of the human facial musculature is still going on with the trend towards fuller differentiation, as emphasized in the text of chapter VII. In the White this process of evolution has apparently progressed further than in other races (compare following figures).

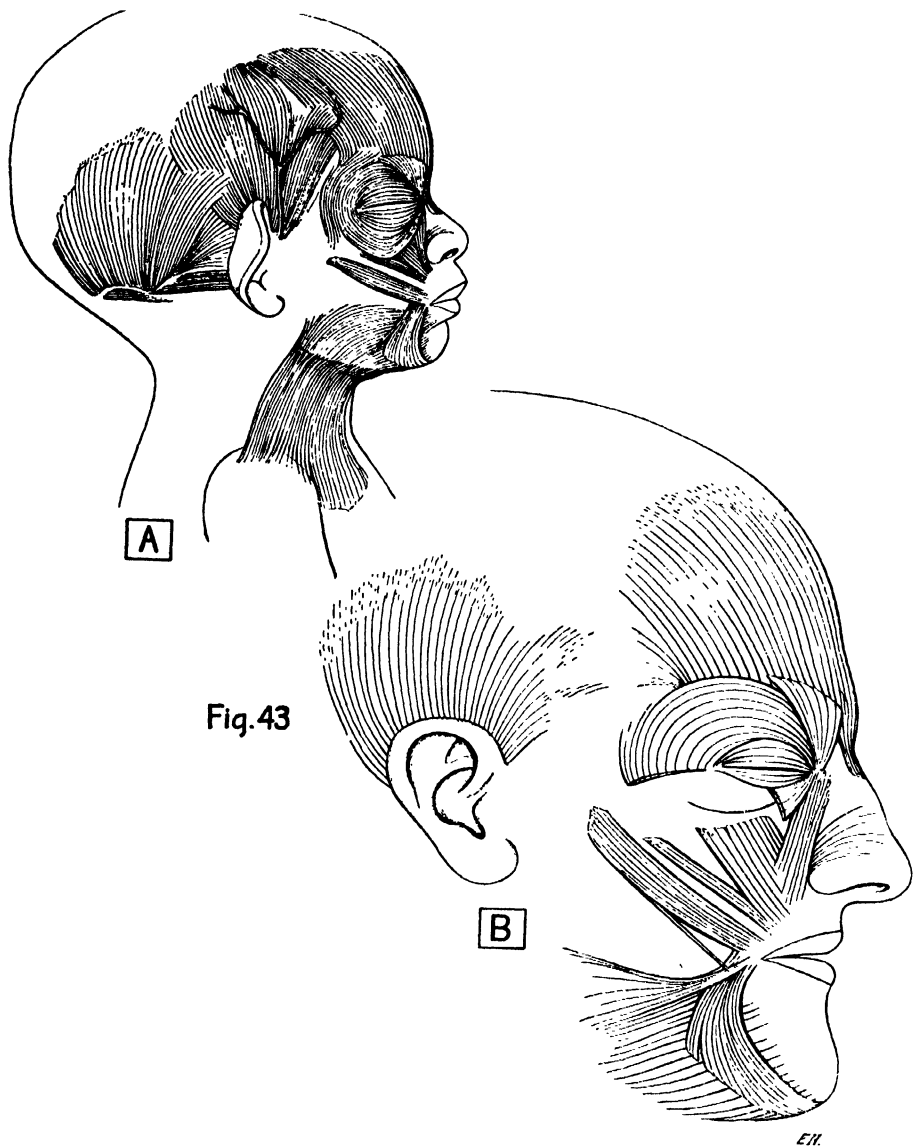


Fig. 43

FIG. 43. ADULT WHITE, CONTRASTED WITH A NEW-BORN WHITE (new-born male of the Collection of the Carnegie Laboratory of Embryology; adult male dissected in the Anatomy of the University of Zürich, Switzerland)

It has already been emphasized that the mimetic musculature of the White is, as a rule, more delicately bundled, less powerfully developed and of lesser extent; but further differentiated if compared with the Negro.

While in the new-born White (fig. *a*) the superficial musculature of the temporal region still shows a primitive extension similar to that in the Negro new-born of fig. 42, it is far reduced in the adult White shown in fig. *b*. Through such reduction the *M. frontalis* became completely separated from the *M. auricularis anteriores superior*. This involution of the muscle complex of the temporal region is part of the postnatal development. Not infrequently however this musculature persists in the adult. All possible intermediate stages may be encountered as in individual variations in the White.

In the mid-face region (figs. *a* and *b*) the *M. zygomaticus* with definite attachment to the zygomatic arch is clearly set off from the *M. orbicularis oculi*, and there is a distinct *M. zygomaticus minor* present, likewise with bony attachment to the zygoma. The latter muscle joins, as caput zygomaticum, the caput infraorbitale and caput angulare to build the "*M. quadratus labii superioris*" of the B. N. A. terminology. This further differentiation of the musculature of the mid-face region is encountered in a prevailing percentage of the White race. It makes its appearance early in fetal life, as seen from previous figures (figs. 40*b* and *c*).

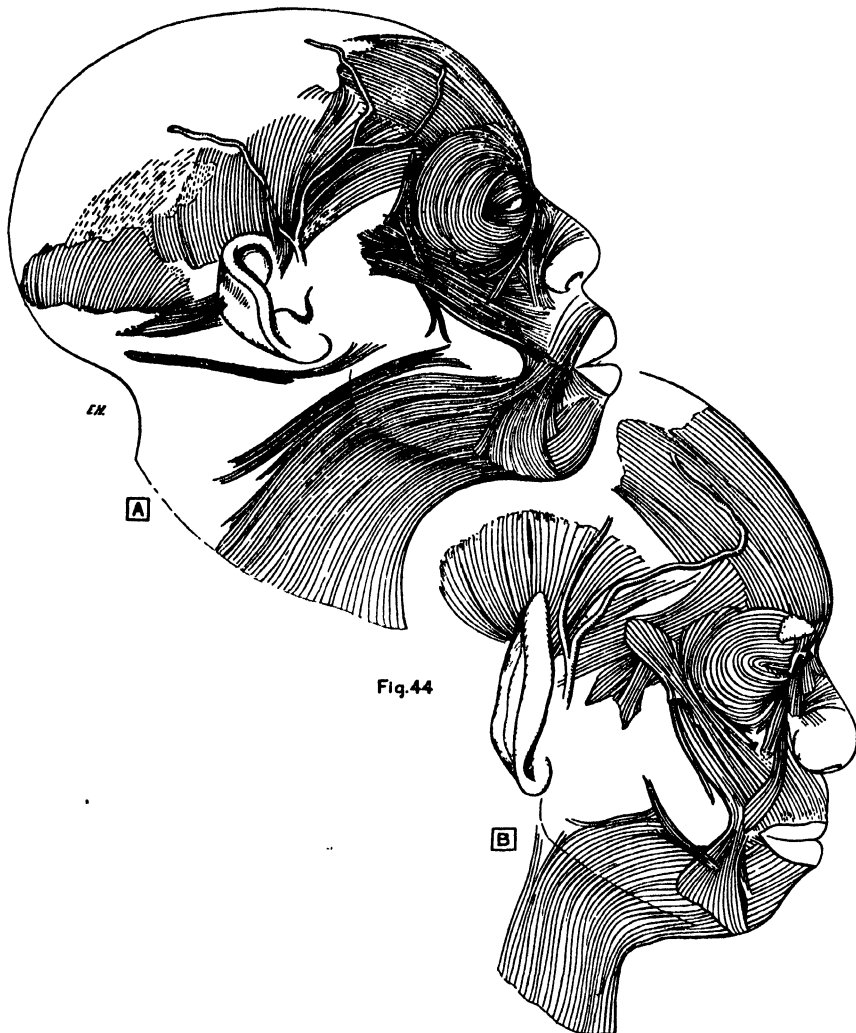


Fig. 44

FIG. 44. ADULT MALE NEGRO AND ADULT MALE AUSTRALIAN, WITH DISTINCT RACIAL CHARACTERISTICS

Fig. a. American Negro (Anatomy, Johns Hopkins University) showing the characteristic vast extension over practically the whole face of the coarsely bundled and powerfully developed mimetic musculature. Most striking are the racial differences (as compared with the adult White of fig. 43) in the musculature of the mid-face, which shows a lack of differentiation. The *M. orbicularis oculi* of the Negro forms a huge powerful compact muscle disc, which far excels the corresponding muscle of the White. The relative width of the supraorbital and infraorbital portions of this muscle is just reversed in the two races, as corroborated through measurements of a large series of cases. In the Negro the width of the supraorbital portion exceeds that of the infraorbital portion. In the Negro, moreover, the marginal bundles of the *M. orbicularis oculi* are in broad primitive connection with the undifferentiated zygomaticus mass, while in the White, in a prevailing percentage of cases, the zygomaticus musculature is more independent of the *M. orbicularis oculi* and usually differentiated into distinct *Mm. zygomatici major et minor*, both with bony origin from the zygomatic arch. In the Negro the preauriculo-temporo-orbital musculature is well developed, while in the adult White, as already mentioned, this muscle complex is generally much reduced. In the Negro the musculature of the bulky lips and cheek walls (not shown in figure) is very massive (compare studies on "Negroes" by previous authors quoted in the literature list).

Fig. b. Australian aboriginal, modified after Burkitt and Lightoller. As to expansion and powerful development these grossly bundled muscles resemble greatly the negroid type; there are, however, characteristic Australian features present, such as the peculiar proportions of the *M. orbicularis oculi*, which differ from those of the Negro, as well as of the White. As Burkitt and Lightoller emphasize, the greatest width of the *M. orbicularis oculi* in the Australian does not lie at the center of the palpebral fissure, but considerably lateral to this. Most striking, moreover, is the unusual extension as far as the lip red of the "labial tractors," i.e. the zygomaticus muscle mass, *M. levator labii superioris proprius* and *M. quadratus labii inferioris* (compare further Burkitt and Lightoller, 1926/27).

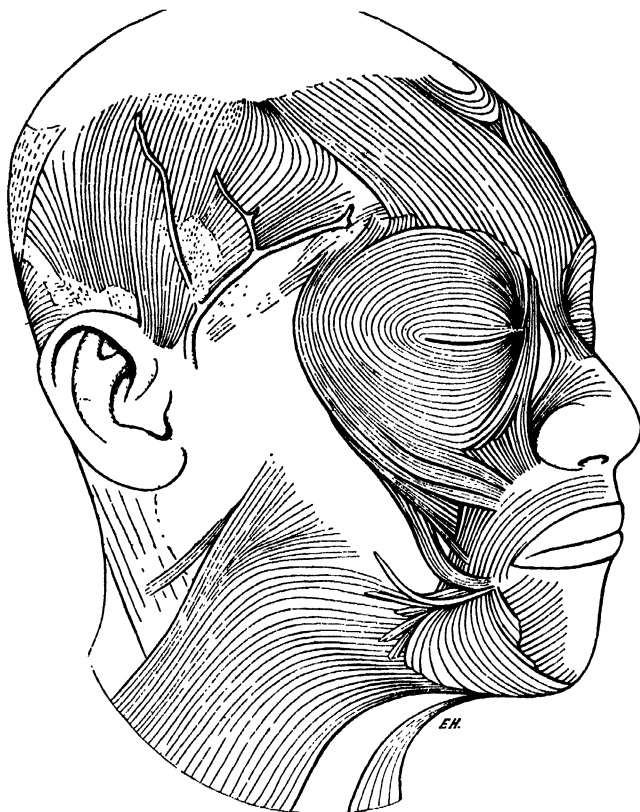


Fig. 45

FIG. 45. ADULT MALE POLYNESIAN (HAWAIIAN) (dissected by THOS. MCP. BROWN, ANATOMY, JOHNS HOPKINS UNIVERSITY)

As in the Negro and Australian the mimetic musculature of this Hawaiian was found more extensive, more powerfully developed, and in the mid-face region less differentiated, when compared with the White. The musculature is compact but not coarsely bundled.

Most striking is the *M. orbicularis oculi*, which forms a powerful muscle disc around the eye. The supra-orbital and the infraorbital portion of this muscle measured vertically from the middle of the palpebral fissure are about of the same width, which equals the lateral extension of the muscle measured from the lateral angle of the eye slit; while the direct broad continuation of the lateral bundles of the *M. orbicularis* into the zygomaticus muscle mass adds considerably to the width of the muscle measured from the middle of the palpebral fissure along a line towards the zygomatic arch. The zygomatico-orbital muscle mass is in its upper part one with the *M. orbicularis oculi*, but in its continuation it splits up into several portions, which partly pass over the orbicularis oris-caninus muscle, partly dip under it, to be inserted into the upper lip; while a very strong, well defined deviating muscle portion joins the *M. risorius* close to the angle of the mouth. This latter portion together with the deep bundles of the zygomaticus muscle mass arises from the zygomatic arch. The insertion of several distinct muscle slips of the zygomaticus muscle mass into the upper lip and angle of the mouth is a noteworthy feature of the Hawaiian, which was even more conspicuous on the left side. It indicates a decided trend towards further differentiation of this musculature.

Peculiar are the proportions of the *M. triangularis*, which arises from the mandible with a very broad basis, while its lateral, marginal bundles form a fan-shaped Risorius muscle.

Note also the vast expansion of the *M. auricularis anterior et superior*. While the orbito-auricular muscle bundles—representing the old phylogenetic connection between the *M. auricularis ant. et sup.* and the *M. frontalis*—are largely deteriorated (in contrast to conditions found in the Negro and Australian (compare figs. 44a and b), the upper part of the *M. auricularis ant. et sup.* is very well developed, and its bundles deviate upward to ascend parallel with the bundles of the *M. frontalis*. This is a progressive feature in the arrangement of the auriculo-temporo-frontal muscle complex in man. It is not infrequently seen in Whites, when this muscle complex persists in greater extent. It also occurs in other races (compare figs. 42, 44a, 46). In a similar extension it has been seen in the Javanese by Koster (1919).

Most unusual in this Hawaiian is the whorl in the upper median part of the *M. frontalis*. Such a formation has never been described, neither in the White or in any other race so far investigated. Future studies of additional Polynesians will prove whether the peculiar features seen in this Hawaiian are constant Polynesian characteristics.

ferences in the two monotreme types (*Echidna* and *Ornithorhynchus*) are obviously the result of divergent specialization.

In the various orders and suborders of the Marsupials and Placentals the superficial facialis musculature has differentiated to different degrees and along many and very distinct lines, a fact which makes

primitive placentals. *Tarsius* is specialized on a primitive, distinctly lemuroid ground plan. It shows unique features in the outer ear (ear cartilage, extrinsic and intrinsic ear musculature of the facialis group) and in the musculature of the eyelids,—mechanisms which in modern *Tarsius* have reached a high differentiation

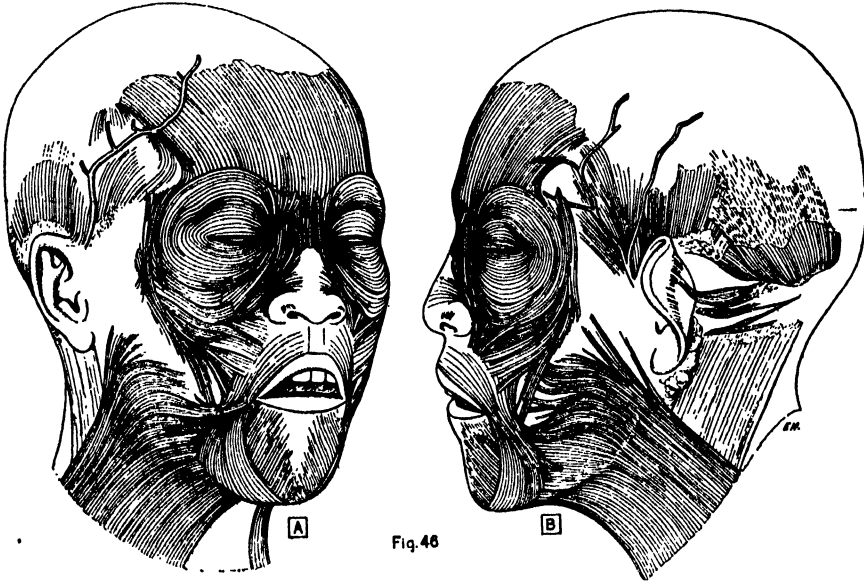


Fig. 46

FIG. 46. ADULT MALE CHINESE (from a joint study by the author and F. H. Langley, Anatomy, Johns Hopkins University)

The Chinese far excels the White as to the vast extension and powerful development of the coarsely bundled mimetic musculature. As in the Negro, Australian and Hawaiian the musculature of the mid-face region shows a lack of differentiation. Striking are the large dimensions of the *M. orbicularis oculi* which, however, in its proportions differs from the other racial types. It is the infraorbital portion which far exceeds the supraorbital portion. The vast extension of the platysma into the region of the face with almost vertically upward tending bundles in front of the ear may likewise be a racial characteristic of the Chinese. Note also peculiar features in the *M. auricularis posterior* and *M. occipitalis* (compare further Birkner, 1905; Kudo, 1919).

the study of the superficial facialis musculature of high systematic value.

The Primates are naturally of special interest. Detailed comparative anatomical studies on the plan of the superficial facialis musculature in this order present important data on the relationship of the various groups of primates. As regards the facial musculature, outer ear, arrangement of facial tactile vibrissae, etc. the lemurs and *Tarsius* link with the other

with corresponding evolution of the central nervous mechanism. These specializations are along an aberrant line, and not at all in the direction towards the higher primates. The findings on the superficial facialis musculature are in favor of the view that the platyrrhines may possibly have shed off from the *Tarsius* stock before the latter began to specialize along the line of modern *Tarsius*. These studies also suggest the possible derivation of the catar-

rhines from lower platyrrhine forms. They bring further data for the understanding of the genetic relationship of the members of the anthropoid stock, and of man's relation to the great anthropoid apes.

The gradual differentiation of the mimetic musculature in the primates in close correlation with the evolution of the corresponding central nervous mechanism led to the elaboration of facial expression, which in man ultimately attained marvelous perfection. There are evidences, however, that the mimetic musculature of man has not yet reached its final structural differentiation.

There exist noticeable racial differences in facial expression which are due to structural differences in the mimetic musculature, skin and subcutaneous tissue, but more so to differences in psychological reactions.

Experiments proved that we have *muscle sense in the mimetic musculature*, which is conducted together with muscle pressure sensibility by the *N. facialis*, though additional postural sensations may be indirectly appreciated through the sensory trigeminus.

With the unique evolution of the superficial *facialis* musculature in the mammals goes hand in hand the evolution of the central structures:

The motor part of the nucleus n. facialis is of corresponding dimensions.

In the Monotremes it is split up into two distinct nuclei, one dorsal and one ventral. The latter has shifted ventralward, but not into a definite ventral position. We have no definite knowledge in regard to the functional rôle of these two nuclei. There is, however, good reason to believe that not only the ventral but also part of the dorsal nucleus is motor.

In the Marsupials and Placentals only a very small part of the facial nucleus,

mainly of visceral nature, retains the original dorsal position, while the other, purely motor part has shifted ventralward (presumably through neuro-biotactic influences) into a position close to the ventral surface of the brain stem. This motor nucleus is enormously increased in size, and subdivided according to the branching of the facial nerve which followed the differentiation of the *facialis* musculature.

The *facialis* musculature of the mammals has its representation in the *facial area of the cerebral motor cortex*. The facial area has frequently been subjected to investigation by many scientists in connection with general investigations on the motor cortex. However, the available data are very incomplete, in part contradictory and not at all correlated with the data from studies on the *facialis* musculature.

The motor *facialis* field is evidently one of the first which in the phylogeny of the mammals became definitely localized in the cerebral cortex. During the embryological development of marsupials and certain placentals however the facial area becomes responsive to electrical stimuli at a considerably later stage than the fore limb area, which in turn precedes the hind limb area. This is presumably due to a developmental adjustment, and not to a phylogenetic sequence.

In Monotremes (*Ornithorhynchus*) the readily responsive facial area in the motor cortex partly overlaps the fore limb area. Here hind limbs or tails have apparently no representation in the motor cortex.

In the Marsupials facial and fore limb areas still overlap to a certain extent. The hind limbs are imperfectly represented, and responses from this area are inconstant.

Within the orders of the Placentals there is a gradual evolution and fuller differentiation of the motor cortex: In the insectivores, bats and rodents the motor cortex

appears to have evolved little above the state found in the marsupials. The ungulates too seem not to have reached a higher differentiation. In the carnivores the various motor areas are well defined, and respond with more elaborate movements. Within the Primates, finally, the motor cortex, including the facial area, attains greatest completeness and highest differentiation in the anthropoid apes and man. Stimulation and ablation experiments in monkeys and apes, combined with physiological studies in man and clinical observations on patients offer an explanation for the well known fact that in central facial palsies the mimetic musculature of the upper part of the face is but little impaired. The explanation offered is that these mimetic muscles are bilaterally represented in the motor cortex. More detailed, special investigations on the facial area of the motor cortex in mammals should be undertaken with a broad knowledge of the peripheral facialis field.

The vast expansion of the motor facialis field in mammals is in striking contrast to the limited *sensory facialis field*, the cutaneous area of which is vestigial.

Together with the superficial facialis musculature, the *cutaneous field of the N. trigeminus* in mammals has attained a remarkably high development, and new functional connections were established between the two fields.

Under the domain of the sensory part of the *N. trigeminus* is the "oral sense" (tactile sense of the snout). In close correlation with the olfactory sense, the "oral sense" has highly evolved in mammals. This is reflected in the central nervous mechanism. As to the peripheral structures which serve the "oral sense" in mammals, the monotremes have developed along their own line, apart from the marsupials and placentals. In both *Echidna* and *Ornithorhynchus* the evolution of the

sensory trigeminus culminates in the high sensitivity of the snout. *Ornithorhynchus* is in this regard unique.

The Monotremes, through their fundamentally different ground plan of the superficial facialis musculature, lack of tactile facial vibrissae and peculiar arrangement of the cutaneous branches of the *N. trigeminus*, just as in so many other points of their organization, are set aside from the rest of the mammals. One is tempted to conclude that the monotremes must have derived fully apart from the marsupials and placentals, from a different group of the theriodont reptiles.

The Marsupials and Placentals, on the other hand, show such striking resemblance in their ground plan of the superficial facialis musculature, in the restriction of the tactile surface of the snout to the rhinarium, in the possession of a tactile vibrissae apparatus actively moved by facialis muscles, in the arrangement of these facial vibrissae, and in the distribution of the cutaneous branches of the *N. trigeminus*, that these characteristics cannot possibly be explained as mere coincidences but must surely be considered the result of common ancestry.

The evolution of the sensory field of the *N. trigeminus* in the marsupials and placentals is closely linked with the acquisition of facial tactile vibrissae. The elaboration of this important head protecting and guiding mechanism was evidently an essential factor in the evolution of the marsupio-placentalian ground plan of the superficial facialis musculature. This in turn goes parallel with the differentiation of the facial area in the motor cortex. In Marsupials and in those placentals where the facial vibrissae are fully developed, vibrissae movements are an outstanding phenomenon in stimulation experiments on the facial area of the motor cortex.

The evolving tactile facial vibrissae

apparatus of the common ancestors of the marsupials and placentals, requiring sensory as well as motor representation in

higher cortical centers, must have played an influential rôle in the early stages of evolution of the neopallium.

LIST OF LITERATURE

A. MOTOR FACIALIS FIELD

I. FACIALIS MUSCULATURE

I. COMPARATIVE ANATOMY, PHYLOGENY AND RACIAL ANATOMY OF FACIALIS MUSCULATURE (CHAPTERS I AND 7)

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THE "CONCEPT OF ORGANISM" AND THE RELATION BETWEEN EMBRYOLOGY AND GENETICS

PART II

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Polonius: Though this be madness, yet there
is method in't.

IN 1925 H. S. Jennings (4) published a little book called *Prometheus*, in the Preface of which he stated that "The exposition of the relations of heredity and environment here given differs from that frequently set forth in the name of genetic science." He added, however, that nevertheless "it is presented as the outgrowth and fruit of the most orthodox genetics of the straitest sect of experimental Mendelism." An anonymous reviewer of this book in a well known biological journal wrote: "In this book the author ascribes greater importance to the environment in determining the nature of living things than most biologists do." That is all he said, beyond mentioning the fact that the book belonged to the "Today and To-morrow Series." Thus there appear to be three entities which have been sufficiently clearly discriminated by genetical science to have received distinct names: (i) one which is called "environment"; (ii) a second called "heredity;" and (iii) a third called "the nature of living things." Moreover, the third stands in the relation of "being determined by" to the first and second. We also learn that there is a *dispute* among biologists about the relative *importance* to be *ascribed* (by the biologists) to the first two entities in their relation to the third. Furthermore, it is clear that

Jennings is in a minority among biologists in respect to the part *he* plays in this process of *ascribing* importance to these entities. It is evident too, that he is conscious of occupying what seems to be regarded as a somewhat unusual position, and so he is careful to explain that this is nevertheless "the outgrowth and fruit of the most orthodox genetics of the straitest sect of experimental Mendelism," although this explanation does not seem to have satisfied the reviewer. But there seems to be *something* in common between the majority and minority, and where they differ is in this process of *ascribing*.

The situation is not, however, so simple as this. In Germany there are eminent writers on genetics who are prepared to challenge, not merely the outgrowth and fruit, but even the root and branch of the straitest sect of experimental Mendelism, at least in the form in which it is presented by what they call the "*Morgansche Schule*." Finally, there is a small band of *franc tireurs* called "Neo-Lamarckians," who keep up a perpetual sniping of all the various more widely held positions—muttering dark hints of superior rival theories of their own which they do not yet appear to have succeeded in formulating clearly. All this is very confusing to the onlooker—especially when he is urged to adopt *one* of the rival theories as a basis for sociological experiments. He should therefore be interested in an attempt to

discover what is common to *all* the contending "sects" and in finding a means of stating this in language which is independent of any one of the rival hypotheses.

There is another interesting passage in Jennings's Preface. He says: "The writer is not one of those who hold that inspired thinking may take the place of experiment in such matters." It may indeed be doubted whether anyone in the twentieth century has held that inspired thinking can take the place of experiment. The tendency is rather in the opposite direction—to suppose that experiment can take the place of inspired thinking. But surely one of these modes of procedure can no more take the place of the other than breathing can take the place of eating or vice versa. They are not two *alternative* procedures but two equally necessary and complementary ones. It is because they are complementary that it is necessary to know what each has to contribute, so that we do not fall into the error of expecting one to do what can only be demanded of the other. It may be that it is because this is not sufficiently understood that there is so much *ascribing*, and *ascribing*, being apparently a somewhat arbitrary and whimsical process, may be responsible for so much indecision and dispute over mere opinions in these matters.

Jennings adds that "The only conclusions at which we can rest are generalized statements of the observed facts. Such it is believed are here set forth." Now generalized statements of observed facts are inductive propositions—such as those expressing the Mendelian 3 to 1 ratio. There is little or no dispute about these. It is not here that ascribing enters, nor are these the conclusions at which Jennings and the others "rest" (if that is a suitable term for describing the present state of affairs). It is in regard to what can be

deduced from such generalized assertions that most of the dispute arises. But there is another aspect of the situation which also occasions dispute, that, namely, regarding what *hypothetical assumptions* we can usefully *impose upon* the inductive data, in order to obtain the intellectual satisfaction afforded by a theoretical interpretation having the maximum generality coupled with the maximum adequacy. These two aspects are not clearly distinguished in the current theories. And, at least with regard to deduction, this seems to be a curious state of affairs, because if we have a set of inductive propositions then there will *also* be a set of propositions which can be validly deduced from them, if the ordinary laws of logic and certain *a priori* postulates are adopted. *If*, therefore, anyone admits the original generalizations, logical laws, and postulates, he is *compelled* also to admit the propositions which can be validly deduced from them. There is no choice in the matter at all, nor is there any place or need for ascribing. How is it then that there is so much dispute? It is customary to suppose that this is satisfactorily accounted for by uttering the one word "complexity"—even by those who assure us in the next breath that growth is a "simple physico-chemical process" (see Part I (14) p. 16). But it would be a pity to allow this word to become a cloak for slovenly thinking. So far as deduction is concerned the answer seems to be that insufficient attention has been paid to this side of biology, and the reason why there is so much ascribing rather than deducing is because the inductive generalizations are often couched in such vague metaphorical language. The very fact that such vagueness is so widely tolerated is a sign that no attempt is made at deduction. For as soon as you do attempt to use vague notions for deductive purposes their shortcomings at once reveal

themselves and you are driven to try to remove them. An inductive generalization will usually contain at least two terms and will assert some relation between them. If one or more of the terms or the relation are at all vague it will be impossible to use that generalization in a deductive argument with any hope of a clear and decisive result. The whole will be like a piece of badly made machinery in which defects are imperfectly compensated for by the use of padding and other make-shifts—corresponding to “ascribing.”

If we analyse out all the different pursuits which go to the building up of a well developed science they will be found to include at least the following:

(1) “Empirical investigation” in the most restricted sense, i.e. the making and recording of actual particular observations, either under or not under experimental, or systematically altered, conditions.

(2) The extension of these observations with a view to discovering whether and how far they can be inductively generalized.

(3) The discovery of clear concepts to embody the inductive generalizations, and the construction of an unambiguous language in which to express them.

(4) The discernment of the type or types of logical order exemplified in a particular field of empirical investigation.

(5) The investigation of the logical properties of types of order as such, i.e. apart from their exemplifications (if any). This includes, but is not exhausted by, pure mathematics as ordinarily understood.

(6) The construction of theories embodying the data yielded by (1) and (2), systematized by the aid of (4), with or without the help of hypothetical entities (e.g. explanations of the “mechanical model” type in physics).

(7) The deductive development of (6) with the help of (5), leading to renewed investigation under (1) with a view to the “verification” of (6) and the checking of (2).

(8) The systematic analysis of the postulates and assumptions underlying (1), (2), and (6).

(9) The critical study of the ontological or “material” concepts employed in (6), e.g. space, time, thing, property, matter, etc.

(10) The study of the problems which present themselves when the question of the “truth” and “objectivity” of scientific knowledge is raised.

It will be seen that as we pass from (1) to (10) we pass from studies of restricted scope in which experiment plays the dominant rôle to others which are common to all the natural sciences and in which the chief requirement is “inspired thinking.” Experiment can do two things: it can provide fresh data to think about, and it can decide between two rival hypotheses (reached by thinking) provided they are of the kind which *can* be decided by experiment, and some of our biological hypotheses are not of this nature.

The precise status of hypothetical entities conceived on the lines of perceptual models with properties “ascribed” to them appears to be very doubtful at the present day. The path of every branch of natural science is strewn with discarded entities of this kind, and there is no richer or more varied collection of them than that which has accumulated in the course of the history of embryology and genetics. The important point is that such entities are useless unless they enter as terms into an abstract logico-mathematical order-system which the empirical data of a given science exemplify. It is this feature which is usually lacking in the use of such entities in biology, in which they are invented *ad*

hoc and merely "do" what their inventor requires of them. Their value seems to be psychological rather than logical: they minister to our craving for the "tangible" and "concrete," but for all that they do not "wear" well. Only the facts and the order systems which they exemplify endure. Considerations based on the modern study of the relation between language and fact point in the same direction. Consequently there is a tendency at the present day to take a less crudely realistic attitude towards hypothetical entities than was formerly the case. Bertrand Russell (8) likens the present situation regarding our knowledge of nature to knowledge of a language which is confined to its grammar and syntax, with complete ignorance of the vocabulary, and what he says about "similarity" of relations is of special interest in this connection. On the other hand it would doubtless be a mistake not to take advantage of any help such hypothetical entities may afford, *so long as the logical links which bind them to what is observed* are not lost sight of, and so long as they are not conceived in such a way as to create obstacles to further progress. There is no occasion to set up the two methods in opposition to one another. In physics they have played into each other's hands in a beneficial manner, although there is sometimes an antagonism between "experimental" and "mathematical" physics. Russell himself writes in another place (9, p. 122):

Physics, as such, should be satisfied when it has ascertained the equations according to which a process takes place, with just enough interpretation to know what experimental evidence confirms or confutes the equations. It is not necessary to the physicist to speculate as to the concrete character of the processes with which he deals, though hypotheses (false as well as true) on this subject may sometimes be a help to further valid generalizations.

On the other hand, on page 194 of the same work he says:

It may be doubted whether science can retain its vitality if it is severed from its root in our animal habits; when set forth quite abstractly it loses plausibility. Induction, for example, is difficult to justify, and yet indispensable in science.

One of the chief difficulties of the modern world depends on the fact that the above mentioned ten studies are, to a very large extent, pursued by different workers independently of one another. And yet, at the same time, no one of them is ever pursued in complete intellectual isolation from ideas which are relevant to the others. No worker under (1), for example, will be entirely devoid of notions concerning the topics dealt with under the other headings. But each science begins with such notions borrowed from everyday life which it only gradually improves upon. These notions are frequently crude and misleading and, from lack of a deliberate critique of concepts and language which might be provided by the sciences under headings (8), (9) and (10), they may continue to obstruct the development of the budding empirical science. If genetics, for example, had started, so to speak, "from scratch" there would never have been so much misunderstanding and dispute. The way in which the language of daily life has kept older notions in countenance is well illustrated by the terms "heredity" and "inheritance." In their legal use these notions involve a three-termed relation as follows. There is first the testator, next the legacy or inheritance, and thirdly the legatee who receives the legacy. The relation of inheritance in this original sense is thus an irreducibly three-termed one. This is the *minimum*, but of course there may also be the family lawyer hovering in the background with his hand-bag containing the deeds. Now it is easy to see how this has influenced biological thought and how misleading it has been. Thus we have had the testator represented by the parents and the legatee

by the offspring, and then, since there is an intermediate term in the former relation it seems to have been felt that the same must be true in the biological one. Consequently we have had a third something, receiving various names, which is *what* is inherited. Even the family lawyer's hand-bag has been represented by the "bearers" or "carriers" of the something which is inherited, (in some cases even the lawyer himself "controlling" things!) But if we put aside such analogies and examine the biological situation we find that we do not have to deal with one which is at all comparable, and the use of the old terms is apt to perpetuate misunderstandings. For in biology the legacy and legatee seem to be one, not two, namely the zygote or fertilized ovum. Jennings remarks that "Possibly we should be better off with no such concept as heredity." But a detailed survey of the damage done by this vague, ill-defined, abstract substantive strongly suggests that "certainly" might here be substituted for "possibly." Jennings points out how "this habit of speech has led to conceiving heredity as something in itself, an entity, a 'force,' something that itself does things—an error that has induced clouds of misconception." But the same is true of many other abstract substantives in biology such as "phylogeny," "life," "function," "adaptation," and many others. It is customary to defend our current linguistic malpractices on the ground of "convenience." But if clouds of misconception are the price paid for convenience the whole purpose of language is frustrated.

The object of this article is to explore the groundwork of embryology and genetics in order to find out what is common to *all* rival theories, and with a view to discovering not what we can plausibly believe, but what we are compelled to infer.

In order to do this we require to disclose (1) the well-established empirical generalizations which are commonly adopted; (2) the a priori postulates which are commonly adopted; and (3) the order-system within which inference in regard to these matters is possible. In Part I it was pointed out that what was there called "hierarchical order" provides such an order-system. This is now worked out in more detail and with greater precision in the hope that it will provide a means of conceiving more clearly some of the perplexities of developmental processes and their relation to genetical problems. We also require a language which is unambiguous, not drawn up in favor of one particular hypothesis, and "fool-proof" in the sense that it prevents one from making senseless assertions. The ideal would be to conduct our discussions in ideographic symbols. We are very far from reaching any of these ideals for a long time to come.

Another ground for the present disputes should be mentioned. At the time of Weismann genetical and embryological problems were not clearly distinguished. At the present day Neo-Lamarckians seem to be primarily interested in "adaptation." Evolution provides yet a fourth topic. These are all obviously related, but until the precise sphere of each is clearly and independently disentangled confusion is only perpetuated by prematurely mixing them up. The present article is only concerned with the first two topics. Part II will be wholly taken up by preliminary explanations and definitions of the notions involved, the inferences and applications being left to Part III.

II

It is unfortunately the case that in any attempt to clarify scientific concepts one is compelled sooner or later to devote earnest attention to questions which are

not biological at all, but which, as was mentioned above, are the concern of all branches of natural science. These questions can be postponed, but they cannot be indefinitely postponed. I will first briefly state what these questions are (or some of them), and then explain the attitude here to be adopted towards them from the biological standpoint. (1) The first is as follows: What is the relation between the entity which is placed on the stage of a microscope and is called a cell, and the entity which a cytologist actually *sees* when he looks through that microscope *at* the entity called a cell? Also, what is the relation between a cell, which is said to be perceived, and such an entity as a "gene," which is not supposed ever to be perceived? (2) The second question concerns the notions which are to be taken as ultimate in the description of nature. The answer to this question had at least the appearance of simplicity so long as it was possible to regard nature as consisting of a collection of small hard spheres just like billiard balls, but too small to be visible even under the microscope, and conceived as being incapable of change save in their spatio-temporal relations; and so long as it was possible to regard tables and chairs and rabbits as aggregates of such spheres, directly revealed in perception as regards shape and size, but with "mental additions" on the part of the observer as regards color, smell, etc. But now the hard spheres have given place to "centres from which radiations travel" and it is difficult to see any simple relation between the latter and "hard spheres." Moreover, it is now seen that the perceived size and shape must be treated on the same footing as the perceived color or smell. Consequently even the "macroscopic" billiard ball is no more perceived than the "microscopic" one in the *same* sense in which the colored shape is perceived.

(3) Thirdly, it will be seen below that the present state of genetical theories is largely determined by the causal postulate, and not simply by "generalized statements of observed facts." This does not seem to be at all generally recognized. It is therefore necessary to make the working of this postulate perfectly clear, and to explain what is meant by calling it "a priori." A flood of light is thrown on many biological controversies as soon as the rôle of the a priori in them is made clear, and it is seen that often the dispute is about something which cannot be decisively settled by an appeal to experience.

(4) Finally, if we are to regard organisms as organized entities we require to know what we mean by "organization," in order to remove the defect in biological theory acknowledged by E. B. Wilson (13) when he says: "we are unable to define precisely the meaning of this vague term." In order to remove something of this vagueness I shall make use of some of the notions discovered by modern mathematical logicians, and it will therefore be necessary to give some explanation of these.

(1) Beginning, then, with the first question: it would obviously be out of place to discuss this topic here. All that one needs to do is to state as clearly as possible the attitude to be adopted and try to adhere to it consistently, but this is not intended to exclude other possible views. I shall call what a zoologist *sees* when he is said to be "looking at a rabbit" or "looking at a cell through a microscope" a "visual sense-pattern," and I shall assume that this is not "the rabbit" or "the cell," which is the subject of physiological propositions, as when we say "This rabbit is respiring," or "This cell is secreting mucin." The visual sense-pattern does not respire or secrete mucin. It is this particular rabbit, or this

call them $p'Aw$ and $p''Aw$. Place $p'Aw$ in E' and $p''Aw$ in yet another and different environment E'' . Then, if the previous rule holds, $p'Aw$ will become $p'A\alpha$, and let us suppose that $p''Aw$ in E'' becomes $p''A\alpha$. Then we have:

$D(p'A\alpha, p''A\alpha).C.D(p'A, p''A)$ and / or $D(E', E'')$

If we assume that the spatial parts of A are uniform in their properties then $p'A$ will not differ from $p''A$, and hence the different behavior of $p'A$ and $p''A$ will be correlated with the difference between E' and E'' . But since $p'A\alpha$ is manifestly different from $p''A\alpha$ they will also be intrinsically different, but this will differ from the case of intrinsic difference between pA and pB in being known to be relationally or environmentally acquired, not an original intrinsic difference.

Suppose, finally, we take another piece ($p'Bw$) from B and, placing it in E'' , observe a change to $p'B\alpha$. Then we shall have $p'A\alpha$ and $p'B\alpha$ in E'' , and consequently with respect to their behavior in E'' (as also in E) A and B are not different. But the causal postulate has already driven us to assume that A and B are intrinsically different, in spite of the fact that this is not manifested in E and E'' . Because two entities are not manifestly different we cannot assume that they are not intrinsically different, but if they *are* manifestly different (under the same conditions of perception) this postulate drives us to assume that they are intrinsically different.

Now this whole procedure rests also on the assumption that whatever part we may cut off from A will have the same properties (in the three environments used) as any other part. Not only have we assumed this, but we have also assumed that A is uniform in its *temporal* parts, so that the properties of A do not change be-

tween the time of cutting off of pA and that of the cutting off of $p'A$ and $p''A$. It is in cases of this kind that we can use the notion of "stuff" or "material" or "chemical substance." The difficulties of biology rest very largely on the fact that neither of these assumptions can be made in regard to living organisms. A living organism is both spatially and temporally heterogeneous and both spatially and temporally organized, and, in so far as this is the case, in applying the notion of "stuff" or "chemical substance" we are abstracting from this heterogeneity and organization. In cases in which this organization is important this procedure will be fallacious if its abstractive nature is not remembered. But in other cases, in which only certain *parts* (later to be distinguished as 'constituents') are involved which are not organized in themselves no such abstraction will be involved. "Living matter" or "living substance" is a muddled notion because the concept of "stuff" or "substance" cannot be applied to a single whole organism, and the constituents to which it can be applied are not usually regarded as "living." This expression is therefore senseless, and its use only the outcome of a thoughtless habit.

We now require to distinguish between two kinds of intrinsic difference. There is first the kind of intrinsic difference we have between the place-dates round the ends of a magnet and the place-dates round the ends of a piece of wood. I shall call this a *relational* difference, since it is correlated with a difference between two other place-dates, namely the place-dates of the magnet and of the wood, and does not persist if the magnet is de-magnetized. But the difference between the magnet and the piece of wood I shall call a *specific* difference, since it does not appear to depend upon a difference between two other entities. The term "specific" will here be

used in this general sense, not in any special biological sense. It is sometimes forgotten that while causal analysis always involves comparison it does not tell us anything absolute about what is compared, but only about their *differences*. That is why we cannot speak of "inherited characters" and "acquired characters," but only of "intrinsic or genetic differences" and "environmental differences" (unless by these expressions are simply meant characters *usually* manifested at birth or hatching and those which may or may not be manifested later).

(4) In order to extend what was said in Part I about biological organization we shall need the following notions belonging to the logic of relations. If we use the symbol " xRy " for " x has the relation R to y " we can define the kinds of relations we require to discuss as follows:

(1) If when xRy we also have yRx , then R is said to be a *symmetrical* relation, e.g. if " x is spouse of y " then " y is spouse of x ."

(2) If when xRy we cannot have yRx , then R is said to be an *asymmetrical* relation, e.g. if " x is father of y " then we cannot have " y is father of x ."

(3) If xRy , then the relation in which y stands to x (which may or may not be R) is called the *converse* of R (here written conv. R).

(4) If we have x, y, z and R such that when xRy , and yRz we also have xRz , then R is said to be a *transitive* relation. But when xRz does not hold, R is called an *intransitive* relation. Thus "greater than" is transitive and "father of" is intransitive. Asymmetrical transitive relations are of immense importance in natural science because they are involved in the generation of series, and the whole possibility of deductive inference and of the application of pure mathematics depends upon them.

(5) If we have x, y, z and two relations R and S , such that " xRy and ySz " then the relation in which x stands to z is called the *relative product* of R and S (written $R|S$). Thus if " x is the mother of y " and " y is the father of z ," then x stands to z in a relation which is the relative product of "mother of" and "father of," i.e. "paternal grandmother of." Relative products are of great importance in science, and the example given is an instance of the use of this notion in genetics.

(6) If " xRy and yRx " then x stands to x in a relation which is the relative product of R and R , and this relation is called the "square" of R (or R^2), and so on for other "powers" of R .

(7) A relation may be two-termed or *dyadic* (e.g. xRy), or three-termed or *triadic* (e.g. $R(x, y, z)$ "Uncle Tom leaves £50 to John") and so on for greater numbers of terms (polyadic or multiple relations).

(8) If " xRy " and there is no other term x' such that " $x'Ry$," and no other term y' such that " xRy' ," then R is called a *one-one* relation. But if " xRy " and " xRy' " but no other term x' such that " $x'Ry$," then R is called *one-many*. And if " xRy " and " $x'Ry$ " but there is no term y' such that " x (or x') Ry' " then R is *many-one*.

(9) If R is any relation the class of terms which stand in this relation to something or other is called the *domain* of R . And the class of terms to which something or other stands in relation R is called the *converse domain* of R . The *field* of R is the sum of the domain and converse domain of R (except in certain cases which need not be mentioned here).

(10) We shall also make use of the following definition of a "system" (see Chadwick (3)).

"The set of entities β is a system with respect to R " means: "If a set δ comprises some, but not all, of the elements of β , and if each entity comprised in δ is also an

element of β , then no matter what set δ may be, at least one entity comprised in δ has either R or the converse of R to some element of β which is not comprised in δ — R being a dyadic aliorelative relation." (An aliorelative relation is one in which a term cannot stand to itself, e.g. "greater than").

The above notions provide us with a means of giving a much more precise account of "hierarchical order" than was given in Part I. Figure 1 is a graphic symbol of a system of entities (represented by the dots) standing in hierarchical order.

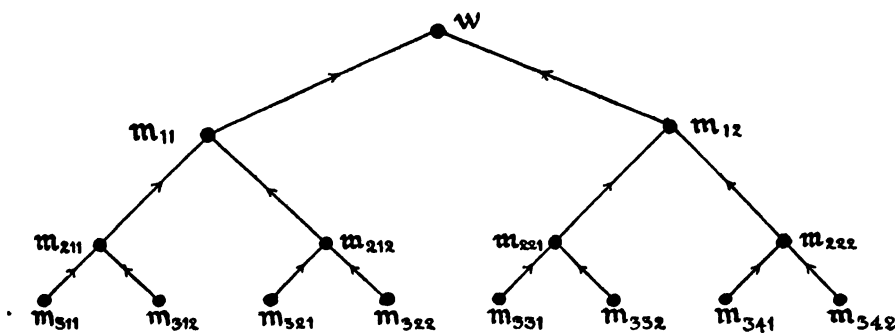


FIG. 1. GRAPHIC SYMBOL OF A SYSTEM OF ENTITIES IN HIERARCHICAL ORDER

The suffix numbers indicate (1) the level, (2) the assemblage within the level, to which a member belongs, and (3) the third number distinguishes one entity of an assemblage from the others. In the first level, where there is only one assemblage, the second suffix number is omitted. In a regular hierarchy in which the number of entities in a level is constant, if N is this number then the number of members of any level L_n is N^n , and each member of L_n stands to W in the relation R_H^n .

It is a system with respect to the dyadic, asymmetrical, intransitive, aliorelative relation symbolized in Part I by " R_H " and here represented in the figure by the barbed lines. It will be seen that this set of entities satisfies the above definition of a system. Also, if we let the symbol " R_H^p " stand for *any* power of R_H , and the symbol " R_H^n " for some one particular, but unspecified, power of R_H (throughout a given context), then it will be seen that the special feature of a system of entities in hierarchical order is that there is one unique entity in the system (W) to which every other entity of the system stands in a

relation R_H^p , but which does not stand in such a relation to any other entity. We can now define a *level* (Part I, p. 8) as the class of members all of which stand to W in a relation which is the *same* power of R_H (i.e. R_H^n) in each case. And an *assemblage* will be the class of members all of which stand to a given member in the relation R_H . A given member is uniquely determined by the assemblage to which it belongs, and the class of members which stand in R_H to it. It will also be seen that although the relation R_H is intransitive, R_H^p is transitive and asymmetrical, since if

we take the three members m_{311} , m_{211} , m_{11} (in the figure) which are such that $(m_{311})R_H(m_{211})$ and $(m_{211})R_H(m_{11})$ then, although it is not the case that $(m_{311})R_H(m_{11})$, it is true that $(m_{311})R_H^p(m_{11})$, and R_H is a value of R_H^p (when $p = 1$). This transitive relation R_H^p also determines a number of other classes. If we consider a given entity of the system, such as m_{12} , then a class of members is constituted by all those members which stand in R_H^p to m_{12} . This class may be called the "posterity" of m_{12} , the term being used in this purely abstract sense. Similarly, there will be a precisely determined class

of members consisting of all those which stand in a relation to a given member, m_{342} say, which is the *converse* of R_H^p . This may be called the class of "ancestors" of m_{342} . These terms, as here defined, are borrowed from mathematical logic, but mathematical logicians have, of course, borrowed them from their particular use in reference to human pedigrees, and this use is simply a particular instance of the exemplification of their more general significance in the actual world. Whitehead and Russell (11) call this relation (R_H^p) the "relation of being related by some power of R ." They denote it by R_{p0} and say:

In a series in which every term (except the first, if there is a first) has an immediate predecessor, and every term (except the last, if there is a last) has an immediate successor, if R is the relation of a term to its immediate successor, R_{p0} is the relation of any earlier term to any later one.

This is the sense in which I use the symbol R_H^p .

We are now in a better position to consider organization, but instead of trying to define "organization" which is probably a hopeless undertaking, we can more profitably attempt to discover what we mean by a "single organized entity" or an "organized event." It is clearly not sufficient to say that by this we mean that the entity is a system in the above sense. If we pour out a bag of coins on the floor it is improbable that they will constitute a system with respect to a given geometrical relation. They will do this only if we arrange them deliberately in some geometrical pattern. But even so the collection as a whole will not constitute a single organized entity in the sense we require. It will not be a "whole" in the sense in which a living organism is a whole. What we have to do is to make clear the difference between, say, a mass of frog's spawn and a

frog blastula. Both are "analysable into cells" but there is clearly a difference between them which we express by saying that the latter is a single whole organism and the former is not. The example of the coins shows that it is not sufficient to say that in the case of the blastula there is some relation between the cells with respect to which they constitute a system and that in the case of the mass of frog's spawn there is no such relation. This is evidently important but there is something more required. And one further requisite seems to be that this relation should be an *internal* relation in the sense that a given term (e.g. a cell) is different when it is in this relation to the other terms from what it is when it is not in this relation. The whole will then change in its properties when it is deprived of a part, and a part will have different properties when removed from the whole from what it has in its place as a part. The whole will have "Gestalt" properties in the sense of Köhler (6). The same principles can be illustrated from chemistry. If we consider a certain gas to be analysable into a finite number of monatomic molecules of two different kinds in equal numbers this will not constitute one whole entity, because there is no special relation between all the molecules, and if the walls of the containing vessel are removed the molecules will diffuse out into the surrounding gases. But if, say, a spark is passed and a chemical change occurs we can conceive this as a consequence of the atoms of the two kinds coming into some special relation in pairs. If we represent the two kinds by a and b and the special relation by R , then we shall have a number of couples aRb , and if R is an internal relation so that now the properties of a and b are different, then the whole collection of couples will exhibit properties which the gas did not previously exhibit. Each couple will be a

new molecule and we shall have a "compound." But we shall still have, not a single organized entity, but only a "quantity of stuff" or a "chemical substance," like the gas, in the sense explained above. But suppose some *further* change occurs and our compound proceeds to "crystallize." If *all* the couples now come into some relation *S* to one another which is internal and in which they do not stand to any other entity, then we shall have a single whole entity resulting from this process. Thus one way at least of conceiving a single organized entity is by regarding it as a system of entities with respect to some internal organizing relation, and as thus, as a whole, constituting an "intrinsic pat-

erty" which endures amid the passing of "place-dates," see above.)

We now have to consider how we are to conceive change in an organized entity so that it may become specifically different from another organized entity. Let us simplify the situation by letting Figure 2a represent a simple organized entity with only four terms *a*, *b*, *c* and *d* standing in relations represented by the lines connecting them. This is merely a "graphic symbol" not necessarily a spatial diagram. It might equally well be written $(a, c, d)R(b)$ indicating that *a*, *c*, and *d* stand in a many-one relation *R* to *b*. Then, with our present ways of thinking, there appear to be three ways in which we can conceive a

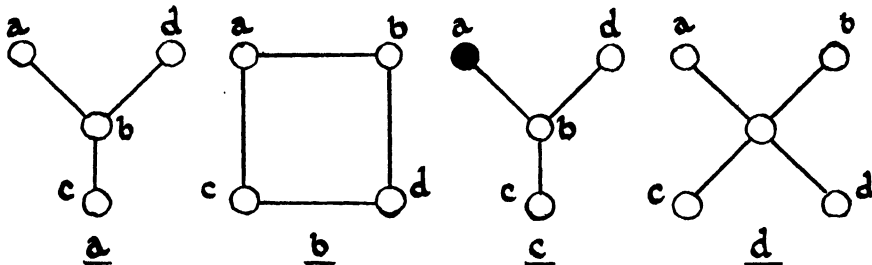


FIG. 2. GRAPHIC SYMBOLS REPRESENTING A SINGLE ORGANIZED ENTITY AND THE THREE TYPES OF CHANGE IT MAY UNDERGO

tern." Whitehead (12) gives the following definition of "pattern"—a term much in vogue in biology nowadays:

An object is a characteristic of an event. Such an object may be in fact a multiple relation between objects situated in various parts of the whole event. In this case the quality of the whole is the relationship between its parts, and the relation between the parts is the quality of the whole. The whole event being what it is, its parts have thereby certain defined relations; and the parts having all the relations which they do have, it follows that the whole event is what it is. The whole is explained by a full knowledge of the parts as situations of objects, and the parts by a full knowledge of the whole. Such an object is a pattern.

(The term "object" is here used in a very general sense for any "character" or "prop-

change in this intrinsic pattern. (1) In the first place (Fig. 2b) we may have a change in the *relations* in which the terms stand to one another. (2) Secondly (Fig. 2c) we may have a change in one or more of the terms themselves. (3) Or, finally, we may have a change in the number of the terms (Fig. 2d). If the relation in which the terms stand is an internal relation then changes of types (1) and perhaps (3) will bring with them changes of type (2). Which alternative (or a combination of two or more) is adopted in the interpretation of nature will of course depend on the requirements of the particular case. Chemistry furnishes examples of all three kinds. Now it will be noticed that if we

assume that a given term undergoes change of intrinsic pattern we have to suppose (under our present ways of thinking) that *it also* is analysable into terms in organizing relations, and then adopt one or more of the same three types of interpretation. And so *ad infinitum* or as long as necessary. If an entity is *unanalysable* we cannot interpret any change in it (if we adhere to our usual ways of thinking) except change in its spatio-temporal relations to other entities. Moreover, we cannot *say* anything about such an entity "in itself" but only about its relations to other entities, because there can be no assertion (and hence no knowledge properly so called) without at least two terms and a relation. Consequently we could say nothing about such an unanalysable entity except in so far as it is a term in some relation to something else. On the other hand we are compelled to assume that it has *some* property or character which distinguishes it from other entities, otherwise it would be a "bare portion of space-time" (see Part I, p. 17). Accordingly, if it were unanalysable this property could not be interpreted analytically in terms of differences between its parts. Thus our current ways of thinking lead *either* (1) to an indefinite regress of analysis, *or* (2) to ultimate entities which are either (a) capable of intrinsic change which cannot be interpreted analytically, or (b) incapable of change except change of spatio-temporal relations. But (quite apart from biology) there is "action at a distance" to be taken into consideration, and it is difficult to see how this is possible between entities which are incapable of change save of spatio-temporal relation (cf. relational difference), not to mention the recondite requirements of modern physics. Moreover colors, smells, sounds, feels, etc., (as well as biologists with their judgments and aspirations) have to be fitted into the

scheme somewhere, and, although it is not the business of biology as such to fit them in, these considerations should warn us that our present ways of thinking are too simple to be adequate except within a certain range of application. It seems probable that we shall have to give up ultimate entities which are incapable of change save for change of spatio-temporal relations, and choose between an indefinite regress of analysis (as one physicist has suggested (1)), or admit entities which are capable of change which cannot be analytically interpreted. Whether the "concept of organism," when it is fully worked out, will provide a better scheme remains to be seen. In Part I. I suggested that we might contemplate the possibility of "determination" of an organic part "from without" as well as "from within," by "synthesis" as well as by "analysis." In other words that, in an organism, the properties of a part depend on the part of *which* it is a part, as well as on the parts into which it is analysable. It is presumably something of this sort that people have in mind when they speak of "organic determination." But it is difficult to bring it into relation with the usual analytical scheme. The difficulty rests on the difficulty of conceiving the relation between a "place-date" and any enduring character it may have on *any* scheme. We are fogged by notions about "things" and their "properties" which we take over from everyday life. There, it suffices to think of things and their properties as standing in a two-termed relation, but scientific investigation shows that we have to do with many entities in multiple relations of great complexity. "Properties" are "shared" between many place-dates, rather than "possessed" by the one of which the property is "predicated." Predication, as Whitehead says, is a "muddled notion." Accordingly we require to

conceive the properties of an organic part or component (see below) as a kind of "surface" or "intersection" (metaphorically speaking) between the components into which it is analysable and the component of which it is a component. We thus have to get out of the habit of regarding only the supposed "ultimate" components as "really real." Otherwise it is quite arbitrary to stop at cells, or genes, or molecules, or even atoms. We require to do justice to each level in the hierarchy of levels.

When an organized entity is divided we appear to have three theoretical possibilities. It may disintegrate into a number of temporally uniform stable elements, or it may be divided into two or more organ-

difference or non-difference between the three entities concerned when one organized entity divides there are five theoretical possibilities. These are represented graphically in Figure 3, in which *a* represents the entity divided, and *b* and *c* represent the products of its division. The continuous lines represent difference and the dotted ones represent non-difference. This scheme will be useful in connexion with types of cell-division.

There are two ways in which we can conceive two organized entities coming into relation to form one organized entity. Either they may do so in such a way that they constitute two terms or components in a new whole, which would then have a different organization from that of either

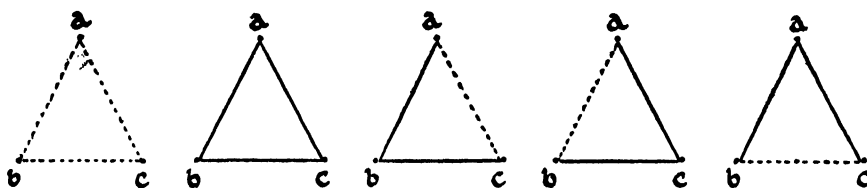


FIG. 3

ized entities which are either intrinsically different from one another (as when a molecule is divided, according to chemical theory), or not intrinsically different from one another or from the original. In the latter case (which appears to occur in the division of some cells, and in *all* cells in so far as the products of division *are* cells) I shall speak of the *spatial repetition* of the original pattern. We have temporal repetition of an intrinsic pattern when it is repeated in every temporal part of an event, i.e. when we have a string of non-simultaneous place-dates all with the same pattern. But with spatial repetition of a pattern we have two simultaneous exemplifications of this pattern in two different events.

From the point of view of the intrinsic

of the two originals. Or, we might have a process of "fusion" in which the two entities lose their singleness and form one pattern of the same type as that of the originals, a possibility which seems to be realized in syngamy.

III

After these preliminaries, which are not special to the biological sciences, we can turn to their applications in biology. Our first task is suggested in the following passages: A. B. Kempe wrote (5):

So far as the processes of exact thought are concerned, the properties of any subject-matter depend solely on the fact that it possesses "form"—i.e. that it consists of a number of entities, certain individuals, pairs, triads, &c., of which are exactly like each other in all their relations, and certain not; these like and

unlike individuals, pairs, triads, &c., being distributed through the whole system of entities in a definite way.

And J. Royce wrote (7):

The prominence of quantitative concepts in our present physical theories is nothing that we can regard as absolutely necessary. There may be, in future, physical sciences that will be highly theoretical, and that will not use quantitative concepts as their principal ones. Yet it is certain that they will use some exact conceptual order-system.

Similarly, C. D. Broad says (2):

All reasoning depends entirely on the logical or formal properties of the objects reasoned about.

diately, and every cell belongs either to the domain or to the converse domain of this relation, or to both. Cells which belong *only* to the converse domain of this relation are called zygotes. We will consider non-zygotes first.

(3) If x is a cell which is not a zygote then there is one and only one cell c to which x stands in the asymmetrical and intransitive relation of "being an immediate division-product of" (symbolized by R_H), and, if attention is confined to binary division, there is one and only one cell c' which *also* stands in this relation to c , (Fig. 4a). Thus every cell which is

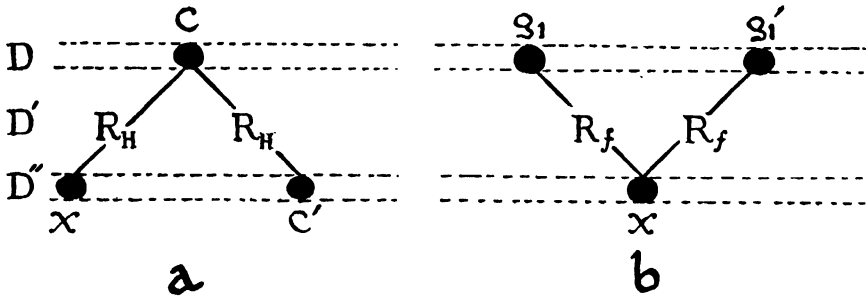


FIG. 4. GRAPHIC SYMBOLS OF (A) A DIVISION TRIAD, AND (B) A FUSION TRIAD

The intervals between the broken lines represent three durations and their temporal relations, but not their relative lengths.

We therefore require to discover, if possible, what are the formal properties of the entities involved in biological reasoning, and the properties of the order-systems into which they enter, and in virtue of which inference in regard to them is possible. Beginning with cells, some of their most important formal properties are as follows:

(1) If x is a cell, x is neither analysable into entities which are cells, nor is it a part of an entity which is a cell.

(2) If x is a cell, it occupies a determinate position in a system of cells (called in Part I a "division hierarchy") which is a system with respect to a relation (symbolized by R_H) to be explained imme-

diately, and every cell belongs either to the domain or to the converse domain of this relation, or to both. Their time relations are such that if D is a duration every moment of which intersects the organized event which is c , then there will be another duration D'' every moment of which intersects x and c' , and there will be a third duration D' every moment of which intersects some phase of the division of c . And these durations (if they all belong to the same family of durations) will be serially ordered, so that D is earlier than D' , and D' is earlier than D'' . And since c is itself a cell it also (if it is not a zygote) will conform to the above properties and will stand

in the relation R_H to one and only one cell belonging to a duration which is earlier than the one to which it itself belongs. If we continue in this way we obtain a chain of such "division triads," and every cell will belong to such a chain and will belong either (a) to both the domain and the converse domain of R_H , or (b) only to the domain of R_H , e.g. a cell which does not divide, or (c) only to the converse domain of R_H , in which case it will be a zygote. (A cell which belongs to *both* the domain *and* the converse domain of R_H may be called a *link*, and one which belongs *only* to the domain *or* converse domain may be called a *terminus*.)

(4) If x is a zygote then it is a cell and a member of a triad of cells, for there is one and only one *pair* of cells g_1 and g_1' to which x stands in the asymmetrical intransitive relation of "being the immediate product of the syngamy or fusion of" (symbolized by R_f), (Fig. 4b). And if D'' is a duration every moment of which intersects x , and if D is a duration every moment of which intersects both g_1 and g_1' , then there will be another duration D' every moment of which intersects some phase of the process of the fusion of g_1 and g_1' . And these durations will be serially ordered so that D is earlier than D' , and D' is earlier than D'' . Thus with respect to time this "fusion triad" may be described as "inverted" as contrasted with the division triad.

Division Hierarchies. Unfortunately these properties are not sufficient to determine a division hierarchy because with reference to a given cell we cannot say whether it will or will not divide. Some cells do not divide. Consequently we cannot include dividing among the essential properties of organized events having the intrinsic pattern of a cell and without which an entity would not *be* a cell. A cell which did not belong to either a division

or a fusion triad would be, from the standpoint of our present knowledge, a "miracle," but a cell which did not divide would not be regarded as anything miraculous. Accordingly we can only say that *if* a cell, which is not a component of an organism (see below), divides, and *if* each of the resulting cells divides, and *if* this process continues, then we shall have a division hierarchy (symbolized by dW) generated, (Fig. 5), (only binary division will be considered in this paper, but the following remarks, with appropriate modifications, will also apply to multiple division).

A division hierarchy is a four-dimensional array of cells standing in hierarchical order, i.e. a system with respect to the relation R_H as defined above. Its chief properties are as follows:

(1) There is one unique member of the system which stands in a relation which is some power of the *converse* of R_H to every other member of the system. This will be symbolized by o . It endures throughout a duration which is earlier than any other duration containing members of the system. If o is a member of a fusion triad it is a zygote. If the two other members of this triad (g_1 and g_1'), which are called gametes, belong to different division hierarchies we have "cross-fertilization;" if they belong to the same division hierarchy we have "self-fertilization." Since g_1 and g_1' belong to a duration which is earlier than that to which o belongs, they cannot belong to the division hierarchy of which o is the first member. If o is not a zygote it will belong to a division triad, and will stand in R_H to some cell which is a component of some spatial hierarchy (see below) of which o is not a component, and we have "parthenogenesis" (in Metazoa).

(2) It will be noted that o corresponds to the entity W of the abstract description of a system of entities in hierarchical order.

(3) When o divides and a division hierarchy is generated from it there are two possibilities: (i) the members remain in organizing relations to constitute components of one whole organized entity and a spatial hierarchy (see below) is gener-

tion which is R_H^p (but not necessarily the same power in each case), and which is such that it does not stand in conv. R_H^p to any cell to which x and y also stand in R_H^p ; z may then be called the *last common ancestor* of x and y .

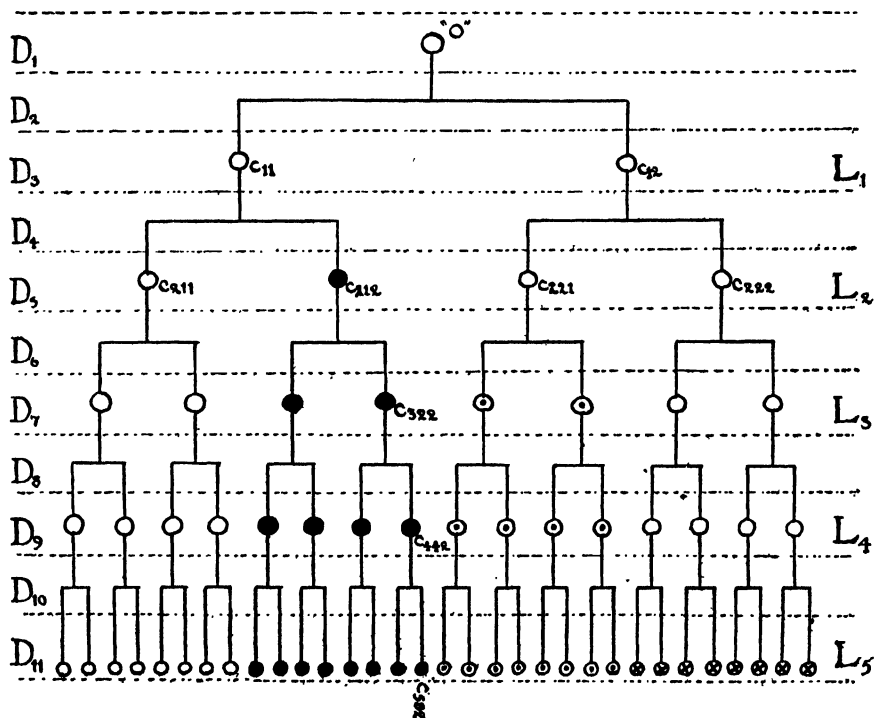


FIG. 5. GRAPHIC SYMBOL OF A DIVISION HIERARCHY UP TO DURATION D_{11}

The intervals between the broken lines represent durations and their temporal order, but not their relative lengths. A given cell is to be conceived as enduring throughout the duration represented by the interval between two adjacent lines between which it is drawn. Thus the cell c_{111} endures from the beginning to the end of D_5 . This figure represents an "ideal" (i.e. logically simplest) hierarchy, in which division occurs simultaneously in every member of each level. In nature this is usually only the case in the earlier levels. The cells represented by the blackened circles constitute a "cell-cone" of which c_{112} is the "apical cell." The cells marked with a dot constitute the cell-posterity of cell c_{211} . The cells marked with a cross constitute the contemporary descendants of cell c_{222} in duration D_{11} . The series of cells c_{442} , c_{222} , c_{212} , c_{112} and o , constitute the cell-ancestors of cell c_{188} .

ated (in Metazoa), or (ii) the members do not remain in organizing relations, but each constitutes one organism (in Protozoa).

(4) If x and y are any two cells in a division hierarchy then either (i) $xR_H^p y$, or (ii) $yR_H^p x$, or (iii) there is some third cell z to which they both stand in a rela-

(5) A division hierarchy is analysable into certain classes of cells which are precisely determined by powers of the relation R_H . Some of these classes are important embryologically and genetically, and it is useful to have names for them. They might all be important if we had the requisite empirical data to make use of

them in a given case. The most important of them are as follows:

(i) The class of cells consisting of a given cell c (which is other than o) and all the cells of the hierarchy which stand in R_H^p to c . This will be called a "cell-cone" because as we go back in time the number of cells in a given duration diminishes to 1, namely to c , which may be called the "apical cell."

(ii) The class of cells consisting of all the members of a cell-cone *except* the apical cell c . This class will be called the *cell-posterity* of c , the latter cell being their last common ancestor.

(iii) The class of cells all of which have the same last common ancestor c , and all of which are termini at a given moment m which intersects the hierarchy (and which is a moment of a duration belonging to the same family as that throughout which o extends). This will be called the class of *contemporary descendants* of c at moment m .

(iv) The class of cells all of which stand to a given cell c in a relation which is conv. R_H^p . This is the class of *cell-ancestors* of c . These cells constitute a temporal series the earliest term of which is o .

(v) The class of cells all of which belong to the same division hierarchy; and consists of *all* the cells of that hierarchy existing at a given moment m (which is a moment of a duration belonging to the same family as that throughout which o extends). This (in Metazoa) will be the "purely momentary" organism of anatomy at the moment m . This brings us to the second exemplification of hierarchical order in the biological realm, namely to "spatial hierarchies."

IV

Spatial Hierarchies. In considering the division hierarchy we are being very abstract. We are dealing only with those aspects of the biological world which flow

from the properties of cells as entities constituting the fields of the relations R_H and R_f . But this is a useful abstraction. In the metazoa (with which we are here primarily concerned) it enables us to refer to the whole four-dimensional organism throughout its history, i.e. as one "long" event. It enables us to define certain classes of cells which are important for embryological description. One such class is that defined above under (v) and comprises the purely spatial or "instantaneous" organism considered in abstraction from temporal "thickness" or "passage," i.e. "at" a certain "stage" of development. And this of course is also an abstraction, because there is no such thing in nature as a purely momentary organism without temporal extension, and no such thing in our experience as a durationless moment. But these "ideals" are also useful abstractions, indispensable in science, and only misleading when we fail to recognize their abstractive nature. We require to keep this constantly in mind and endeavor to combine the results of both methods of abstraction.

The class of cells defined under (v) above is called a "spatial hierarchy" because it is analysable into a system of entities in hierarchical order. In this case the entity W is represented by the whole spatial organism, and the other entities of the system are represented by its spatial "parts." The relation R_H is the relation between, say, a given cell and the cellular part of which it is a part, or between a given cellular part and the whole (in certain cases) of which it is a part, and so on, (Fig. 6). But the term "part" is very ambiguous, and it is important, from the standpoint of biological organization, to discriminate clearly between some of its meanings. In the first place we may mean a "bare part"—a "bare portion of space-time"—considered in abstraction

from any character or intrinsic pattern it may have. But the two kinds of parts we require to distinguish from the biological standpoint are what I shall call "components" and "constituents." A *component* of an organism will be defined as a spatial part which is an *assemblage* of the spatial hierarchy (see below) and is therefore to be conceived as including no components of the hierarchy other than those to which it stands in a relation which is the converse of R_H^P (in the spatial sense or application of R_H). Thus a nucleus is a component, a cell (except ϕ) is a component, and the entire central nervous system

part of an organism which lies outside the hierarchical order, i.e. does not stand in conv. R_H to components, e.g. cartilage or bone matrix, connective tissue fibres, blood-plasma, yolk and secretion granules. It is in relation to constituents of this kind as opposed to components that the notion of "chemical substance" can be most safely applied because, as already explained, this notion does not take account of the hierarchical or any other organization, but applies to entities in which the spatial distribution of properties or character is uniform, so that one spatial part can be regarded as a "fair

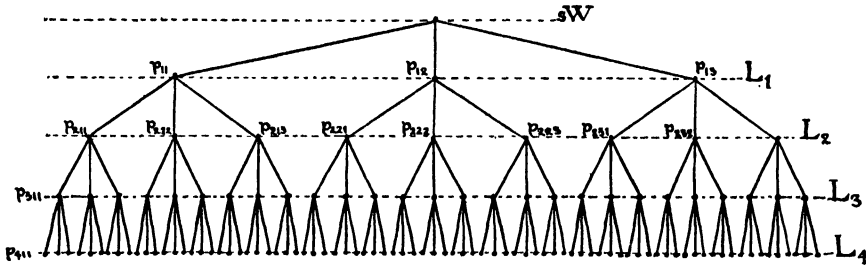


FIG. 6. GRAPHIC SYMBOL OF A SPATIAL HIERARCHY (sW)

In spatial hierarchies there is of course no fixed number of members in an assemblage, hence the number depicted here (3) is of no general significance. Also the nature of the components of a given level will differ according to taxonomic position or according to the temporal position in the division hierarchy. Thus in Protozoa L_1 would represent cell-components of the first order. In a gastrula L_1 would represent the primary germ-layers, L_2 would represent cells, and L_3 the level of cell-components of the first order. In later stages L_1 would represent cellular components of the first order, L_2 those of the second order, and so on.

of a vertebrate would be a component. Thus we have (i) cell-components, (ii) components which are single cells, and (iii) cellular components. If a cellular component has components which are cellular it is a compound cellular component. Thus the cells of a given spatial hierarchy can, theoretically, be regarded (i) from the point of view of their distribution among cellular components, and (ii) from the point of view of their distribution among cell-cones. A *constituent*, on the other hand, is either any arbitrary part taken without regard to the hierarchical order, e.g. a beef-steak, or it is a spatial

sample" of the whole, or "some" is representative of "all."

We can now distinguish between *temporal* parts or "slices" of a four-dimensional division hierarchy (in Metazoa) and *spatial* parts. A temporal slice is always a whole spatial hierarchy, whereas a spatial part is either a component or a constituent, or, it may be, a "bare" part, of a spatial hierarchy. But of course a *purely* spatial part is just as much an abstraction as is a purely spatial organism. Where there is any risk of ambiguity it will be desirable (for the present) to use the symbol $R_H(s)$ for the hierarchical rela-

tion in spatial hierarchies, and $R_H(\mathcal{A})$ for the corresponding relation in reference to division hierarchies. A spatial hierarchy will be symbolized by " \mathcal{W} ". The following are some of its chief properties.

(1) Since a spatial hierarchy is defined as a class of cells it may be a class with only one member. This is the case during the earliest duration of the division hierarchy, when there is only one cell, namely ϕ . In all other durations the spatial hierarchy contains more than one cell, in Metazoa. But in Protozoa cells do not belong to the domain of $R_H(x)$, since the level of organization in a spatial hierarchy does not rise above that of a cell.

(2) A spatial hierarchy (and also a cellular component) is analysable into (i) n cells, of (ii) m kinds, and into (iii) the organizing relations in which the cells stand.

(3) If every cell in a spatial hierarchy stands to it in the relation R_H there are no cellular components.

(4) If a cellular component stands to the whole spatial hierarchy in the relation R_H it is a cellular component of the first order. If it stands to \mathcal{W} in a relation R_H^2 it is a cellular component of the second order, and the component of which it is a component (and to which it stands in R_H) will be a compound cellular component.

(5) Similarly, if a cell-component stands to a given cell in R_H it is a cell-component of the first order, if in R_H^2 it is a cell-component of the second order, and so on.

(6) If we describe a compound cellular component merely in terms of its cells we are abstracting from any special properties they may exhibit as members of one of its second-order components.

(7) Just as in the division hierarchy, so here also, the powers of the relation R_H (in this case $R_H(x)$) determine certain classes (in this case classes of components). These are as follows:

(i) The class of all parts which stand in R_H^p to \mathcal{W} , i.e. the class of all components ("living parts") of an organism.

(ii) The class of components all of which stand to a given \mathcal{W} in a relation which, in each case, is the *same* power of R_H , i.e. a level.

(iii) The class of components all of which stand to a given component in a relation R_H^p , i.e. the class of components of a component, or the (spatial) "posterity" of a component.

(iv) The class of components all of which stand to some component p , which is a component of \mathcal{W} , in a relation which in each case is the same power of R_H (i.e. R_H^n), and is thus a selection from a level limited with respect to the relation of its members to a given component.

(v) The class of all components which stand in the relation R_H to a given component, i.e. a particular case of (iv) when $n = 1$, hence an assemblage. (Classes (iv) and (v) simply represent different degrees of analysis of a given component).

(vi) The class of all components which stand to a given component p in a relation *conv.* R_H^p , i.e. the (spatial) "ancestry" of a component. For example, a given chromosome will belong to one and only one cell, and this will belong to one and only one cellular component of the n th order (if such there be in the hierarchy), and so on.

(vii) The class of all parts which do *not* stand in *conv.* R_H to components. This is the class of constituents which are not analysable into components, thus excluding beef-steaks but not excluding cartilage matrix. Such constituents "lie outside" the spatial hierarchy, but not "outside" the organism. Thus an organism possessing such constituents cannot, as a "whole" be a system *simply* with respect to the relation $R_H(x)$. From this point of view a molecule, or an atom, or an electron

(whatever interpretation may be given to those terms) will, if it belongs to the (spatial) "posterity" of a given component, be just as much "alive" as a cell, and one which does not belong to the posterity of a component will be "dead." There is no sense whatever in asking whether this is "true." It is merely a *partial* statement of a possible meaning of the term "alive," as applied to a part. It gives expression to one aspect of living organisms which the "concept of organism" embraces, to the fact, namely, that the whole requires its components in order to "be alive," and the parts require the whole in order to make their particular contribution to it in virtue of which it is "alive." In other words, the term "living" applies not to the components as such but to the components in their organizing relations in virtue of which they display their special *relational* properties (cf. Part I, p. 15). If these relations are internal relations this must be so, but whether, in a particular case, this is so can only be discovered by experiment. It is in view of such considerations that I shall restrict the term "environment" to the environment of a whole organism, or of a component isolated from the whole. If this term is used indiscriminately for the environment of a whole and for the specific organizing relations in which a component stands when it *is* a component, then the important difference between the two situations is obscured, and, in cases where this difference cannot safely be ignored, avoidable difficulties will be created.

V

Genetic Hierarchies. We now reach the third exemplification of hierarchical order in the biological realm (Fig. 7). The symbol " dW " has been used for a division hierarchy, and " o " for its first unique member. Where, in an argument, we

require to distinguish different division hierarchies we can put a numerical suffix after the symbol dW , and a corresponding suffix after the " o " from which it is generated. The symbols " g_1 " and g_1' " have been used for the two gametes from the fusion of which a given " o " results. Where it is necessary to distinguish a zygote by a suffix number the corresponding pair of gametes can be distinguished by placing in brackets with a corresponding suffix number after them. Instead of saying "the zygote o_1 results from the union of the gametes g_1 and g_1' ," we can express this more concisely by " $(o_1)R_f(g_1, g_1')_1$ " (the comma being read "and"). We can use the symbols g_1, g_2, g_3 , etc., for different gametes of the same (male) division hierarchy; and the symbols g_1', g_2', g_3' etc., for different gametes of another (female) dW . For any cell of a division hierarchy other than an o -cell or g -cell the symbol " c " is used, with or without a numerical suffix as required. Instead of saying "the cells c_2 and c_3 both result from the division of c_1 ," we can express this more concisely by putting " $(c_2, c_3)R_H(c_1)$ ". All these notions have perfectly clear meanings and occur so frequently in embryological and genetical discussions that it is profitable to have symbols for them which allow the successive steps in an argument to be stated in a compact, uniform and precise form, as will be shown in Part III. A genetic hierarchy can be described as follows:

(1) If o_1 is a zygote (Fig. 7), then there is one and only one pair of gametes (g_1, g_1')₁ such that $(o_1)R_f(g_1, g_1')_1$.

(2) And there will be one and only one zygote o_{11} such that $(g_1)R_H^p(o_{11})$, and there will be one and only one zygote o_{12} such that $(g_1')R_H^p(o_{12})$.

(3) Consequently, there is one and only one *pair of zygotes* (o_{11}, o_{12}) to each member of which o_1 stands in a relation which is

the *relative product* of R_f and $R_H^p(d)$. This relation has the same formal properties as the *converse* of the relation R_H , and we can therefore call it *conv. $R_H(g)$* , since it is the converse of the R_H relation for genetic hierarchies.

(4) Now since o_{11} and o_{12} are zygotes they will also stand in similar relations to other zygotes. There will be a pair of zygotes (o_{211} and o_{212}) to which o_{11} stands in *conv. $R_H(g)$* , and a pair of zygotes (o_{221}

o_{221} , and o_{222} represent the four members of the level next below the first, and so on. The four zygotes last mentioned will stand to o_1 in a relation which is the square of $R_H(g)$.

(6) But it will be seen that this system differs from the other hierarchies we have considered in being only a *selection* from a wider system which has the character not of a hierarchy but of a *network* of intersecting hierarchies. For o_1 may not be the

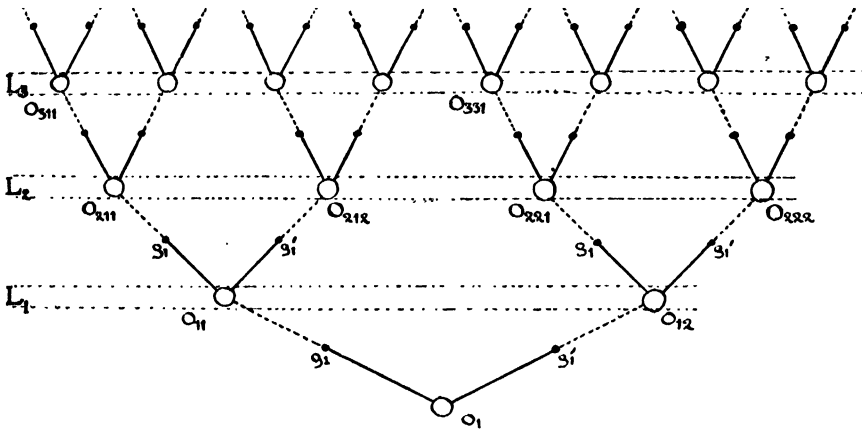


FIG. 7. GRAPHIC SYMBOL OF A GENETIC HIERARCHY WITH RESPECT TO THE ZYGOTE o_1

The relation $R_H(g)$ is a relation between zygotes, but this relation is the relative product of two relations, namely the converse of R_H^p (between a given zygote and a certain gamete g_1 , belonging to its cell-posterity), indicated by the broken lines, and the converse of R_f (between g_1 and the zygote into the constitution of which it enters), indicated by the continuous lines. Consequently, although the gametes are not terms in the relation $R_H(g)$ and are not members of the hierarchy, they are shown in the figure as the intermediate terms in the relative product. Durations are not indicated, but it is evident that the members of a given level L_n (although they may belong to different durations) will extend through durations all of which are earlier than durations extended over by members of levels higher than L_n , and later than durations extended over by members of levels lower than L_n .

and o_{222}) to which o_{12} stands in *conv. $R_H(g)$* ; and so on.

(5) Consequently a given zygote o_1 determines a system of zygotes which is a system with respect to the asymmetrical, intransitive relation $R_H(g)$, i.e. the relation in which o_{11} and o_{12} stand to o_1 . And since this is an instance of the hierarchical relation this system will constitute a hierarchy of which o_1 represents the entity "*W*," o_{11} and o_{12} represent the two members of the highest level, o_{211} , o_{212} ,

only zygote standing in *conv. $R_H(g)$* to o_{12} and o_{11} , and similarly o_{11} may not be the only zygote standing in *conv. $R_H(g)$* to o_{211} and o_{212} . Consequently we can only speak of a hierarchy *with respect to a given zygote*. We can express this by saying that a genetic hierarchy (as here defined) is a selection from the field of the relation $R_H^p(g)$ obtained by taking a given member of the field (such as the zygote o_1) together with all the members which stand in $R_H^p(g)$ to it. Thus two or more gene-

tic hierarchies may be identical except for the entity corresponding to " W ," and the class of zygotes which can be substituted for the zygote corresponding to " W ," while leaving the rest of the hierarchy unchanged, will consist of "brother" or "sister" zygotes. This class gives *one* meaning of the term "generation." We can define a generation as a class of zygotes all of which stand in conv. $R_H(g)$ to a given pair of zygotes, and the term can then be extended to the division hierarchies generated from them. This is the sense in which an " F_1 generation" is a generation, but not necessarily that in which an " F_2 generation" is a generation.

(7) Since a genetic hierarchy is a selection from a network there are other ways in which the selection might be made. We might treat a given pair of parental zygotes as representing " W ," and their offspring as the "first level," and so on (as was mentioned in Part I), but the above method is simpler and brings out clearly the analogy with the other exemplifications of hierarchical order. The genetic hierarchy is "inverted" with respect to time as contrasted with the division hierarchy.

(8) Another complication is introduced by the fact that the same member may occur twice in a given hierarchy. For example, o_{331} may be identical with o_{311} , these being merely different symbols for the same zygote. In this case o_{211} and o_{221} (if they were both "male") would be "half-brother" zygotes. ("Maleness" of course has different senses, and a zygote is not "male" in the same sense in which an adult slice of its division hierarchy may be "male").

(9) In cases where "self-fertilization" is the rule, so that g_1 and g_1' both stand in $R_H^p(d)$ to the *same* zygote we should obtain a different system of zygotes in which the zygote-ancestors of a given zygote

would constitute a *series*. The system would be a hierarchy which would not be inverted with respect to time as contrasted with the division hierarchy. The same graphic symbol which serves for the latter would then serve for the former, except that the number of members in an assemblage would not necessarily be limited to 2, (as it is when division is binary). In what follows the term "genetic hierarchy" will refer to systems of the first or "inverted" type.

(10) It will be seen that powers of the relation $R_H(g)$ determine certain classes of zygotes which are exactly analogous to the classes determined by powers of R_H in the other hierarchies. These are given in the table below.

(11) The above description of a genetic hierarchy (gW) will, like the description of a division hierarchy (dW), apply both to Metazoa and to Protozoa in which syngamy occurs.

VI

It would be a great mistake to expect too much of "hierarchical order," or to suppose that everything can be got out of it. But it does appear to be *a* type of order underlying embryology and genetics, and one which determines the lines along which biological inference moves in relation to these topics. Incidentally the above instances of its application illustrate some points of scientific methodology which were mentioned in Part I (p. 5). These preparatory clarifications (which do not profess to be by any means exhaustive) have occupied the whole of Part II. But the proof of the pudding is in the eating, and in Part III it should be possible to state clearly the relations between the various sciences which are here involved, and to develop deductively the consequences of well established generalizations in embryology and genetics without

reference to any particular hypothesis, and without too much recourse to "ascribing," in order to discover what is com-

mon ground between existing rival speculations, and how far their differences are traceable to avoidable obscurities.

Three exemplifications of hierarchical order in biology. Classes determined by powers of R_H

IN THE ABSTRACT	IN dW	IN sW	IN gW
(1) Members standing in R_H^1 to W .	Cell-posterity of an α -cell.	Spatial "posterity" of a whole.	Zygote-ancestors of a zygote.
(2) Members standing in R_H^n to W (where $n > 1$).	Cells of level n .	Components constituting level n .	Zygotes of level n .
(3) Members standing in R_H to W .	First two cleavage cells (Metazoa).	Cellular components of the 1st order ("organ system").	Parental zygotes.
(4) Class (1) + W .	dW .	sW .	gW .
(5) Members standing in conv. R_H to W .	Null.	Null.	Null.
(6) Members standing in R_H^p to a given member m .	Cell-posterity of a cell c .	Components of a component p .	Zygote-ancestors of a zygote o .
(7) Members standing in R_H^n to a given member m (where $n > 1$).	Sub-class of a level limited by relation of its cells to a given cell c .	Components of level n which are components of a given component p .	Parental, or grand-parental, or . . . -parental, etc., zygotes of zygote o .
(8) Members standing in R_H to a given member m (assemblage).	Immediate division products of a cell c .	Components (belonging to level $n - 1$) of a component belonging to level n .	Parental zygotes of a given zygote o .
(9) Class (6) + m .	A "cell-cone."	A component.	A gW with respect to zygote o which stands in $R_H(g)$ to some other zygote.
(10) Members standing in conv. R_H^p to a given member m .	Cell-ancestors of a given cell c .	Spatial "ancestors" of a component p .	Descendants of a zygote o limited to a given gW .

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NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of THE QUARTERLY REVIEW OF BIOLOGY, 1901 East Madison Street, Baltimore, Maryland, U. S. A.

BRIEF NOTICES

EVOLUTION

L'ÉVOLUTION EN BIOLOGIE. *Fondation "Pour la Science."* Centre International de Synthèse. Première Semaine Internationale de Synthèse. Premier Fascicule.

Exposés by Maurice Caullery, Émile Guyénot, and P. Rivet. *La Renaissance du Livre*

5½ x 8; xv + 84 (paper) Paris

The Centre International de Synthèse (*Fondation "Pour la Science"*) appears to be the equivalent of an extremely high-brow American Open Forum. This little volume is its first publication. Two distinguished biologists and an equally distinguished anthropologist lectured pleasantly and shrewdly on different aspects of evolution and here are the lectures and the discussion of them from the floor. Caullery starts by reviewing, in a masterly way, the development and present condition of our ideas about evolution, and ends, as so acute a thinker is bound to, on an agnostic note as to the mechanism of evolution, with a pessimistic overtone as to the improbability of any speedy solution of

the problem. Guyénot next reviews the bearing of modern genetic research, particularly that on mutations and chromosomes, on the evolution problem. Finally Rivet sums up, with the precise, critical realism of French science at its best, what is known of the evolution of man. Again the conclusion reached falls far short of ruddy optimism. The truth is, and Rivet says so, that the fossil man branch and the fossil ape branch of the evolutionary tree both plunge separately down into the remote past, and there is not the faintest trace of factual evidence to tell us at what epoch they were joined together in a common trunk, if ever. Rivet ends by saying that while Karl Vogt maintained that he would rather be a perfected ape than a fallen angel, we now know that man is neither of these. This book should not be allowed to fall into the hands of a Fundamentalists. At the same time, however, the publishers of the various series of dollar tracts, about science and other things present and future, are missing a good bet if they do not publish a translation of this little book.

EMBRYOLOGY AND EVOLUTION.

By G. R. de Beer. Oxford University Press
\$2.00 $4\frac{3}{4} \times 7\frac{1}{4}$; viii + 116 New York

This little book is the result of a "simmering revolt" on the part of the author when he came to the realization that the "theory of recapitulation was not all that it claimed to be." In presenting his arguments against this theory and for a return to the earlier concepts of von Baer the writer states his case with simplicity and directness. An excellent book to put in the hands of advanced students.



GENETICS

THE HORSE OF THE DESERT.

By William Robinson Brown (with an Introduction by Major General James G. Harbord and Henry Fairfield Osborn).

The Derrydale Press

Regular edition \$27.50 New York
De luxe edition \$100.00

$9\frac{1}{2} \times 12\frac{1}{2}$; xxviii + 218

Sad experience teaches a reviewer to look with a bilious eye upon luxuriously produced volumes in quarto written by rich men about their hobbies. They are apt to be such dilute and poisonous pap that even the condiments of beautiful paper, typography and illustrations cannot make them digestible. This volume on the Arabian horse is a rare and notable exception to this class of books to which apparently and superficially it seems to belong. It is a meaty and salty treatise. The author is now the leading breeder of the Arabian horse in America, and has gone into the vitals of his hobby with unusual depth and thoroughness. Every library of genetics should most certainly have this volume on its shelves.

The book opens with an account of a trip to Arabia to purchase breeding stock.

A Ford sedan furnished motive power. In a fairly wide acquaintance with the travel literature about Arabia the reviewer has never come upon so completely debunked an account of that interesting country and its inhabitants as this appears to him to be—and he is not forgetting Doughty or T. E. Lawrence. It is quite simply and therefore charmingly written, and plainly is not only truthful but true. One's only regret is that there is not more of it.

The book then goes on to a useful account of the origin and history of the Arabian horse, its anatomical, physical and mental qualities, and its blood lines in Arabia, all showing real, thorough scholarship, and a rich knowledge of Arabian lore. Other breeds of horses are then discussed in their relations to the Arabian. A chapter gives shrewd and detailed advice about purchasing breeding stock in Arabia. The final chapter discusses the usefulness of the Arabian, especially for cavalry purposes. A long bibliography and a detailed index complete a notable book, which is beautifully printed and superbly illustrated.



ÉTUDES SUR LES MALADIES FAMILIALES NERVEUSES ET DYSTROPHIQUES.

By O. Crouzon.

Masson et Cie

55 francs

Paris

$6\frac{1}{2} \times 9\frac{1}{8}$; viii + 385 (paper)

This is an interesting volume, which will be useful to all students of human biology for reference, on the nervous and dystrophic diseases recognized to be familial in their incidence. Seventeen chapters are devoted to the familial nervous diseases, and fifteen to the familial dystrophic. The discussion throughout is essentially descriptive in character,

rather than philosophical. The author catalogues and describes the known facts with admirable precision and compactness. The author obviously knows the literature of his subject thoroughly. It is a pity that he did not increase the usefulness of his book by including a systematic and comprehensive bibliography.



CONTRIBUTIONS TO THE GENETICS OF *DROSOPHILA SIMULANS* AND *DROSOPHILA MELANOGASTER*. *Carnegie Institution of Washington Publication No. 399.*

By A. H. Sturtevant, C. B. Bridges, T. H. Morgan, L. V. Morgan and Ju Chi Li.

Carnegie Institution of Washington, D. C.

\$4.00 (paper)

\$5.00 (cloth)

6 $\frac{1}{2}$ x 10; 296

Eight papers in this volume record hitherto unpublished data on the genetics of *Drosophila* by Morgan and his associates. The results reported may be said, in the main, to clarify and amplify points already known from the author's earlier work, and to "complete the record."



VERSUCH EINER THEORIE DER GENKOPPELUNG. *Bibliotheca Genetica Band XV.*

By K. v. Kőrösy.

Gebrüder Borntraeger

40 marks

Leipzig

7 $\frac{1}{2}$ x 10 $\frac{1}{2}$; xii + 272 (paper)

A detailed discussion, primarily mathematical, of the theory of linkage and of chromosomal mechanics in relation to genetics generally, covering similar ground to that of the earlier work of Haldane and Jennings but proceeding to wider generalizations. The volume is dedicated to the memory of Jacques Loeb. Its observational data are drawn from the work of Morgan and his colleagues.

LA VARIATION ET L'ÉVOLUTION.

Tome I. La Variation.

By E. Guyénot.

Gaston Doin et Cie

32 francs

Paris

4 $\frac{1}{2}$ x 7; xxviii + 457 (paper)

A well-written semi-popular discussion of the results of modern genetics, especially concerning itself with the mutations of *Drosophila*. There is a bibliography of 36 pages and an index.



GENERAL BIOLOGY

EDUCATIONAL BIOLOGY.

By W. L. Eikenberry and R. A. Waldron.

Ginn and Co.

\$2.48 5 $\frac{1}{2}$ x 7 $\frac{1}{2}$; viii + 549 *Boston*

EDUCATIONAL BIOLOGY. *The Contributions of Biology to Education. A Textbook for Teachers' Colleges and University Schools and Colleges of Education.*

By John C. Johnson. *The Macmillan Co.*

\$3.00 5 $\frac{1}{2}$ x 7 $\frac{1}{2}$; xx + 360 *New York*

Most colleges, universities, and normal schools now require of students completing two and four year teacher training courses some type of instruction in Biology as a basis for the study of the principles of education, educational psychology, educational sociology, nature study, elementary science, health education, etc. This instruction is also intended to be vocational, that is, of practical value in the schoolroom as an aid in the solution of problems of behavior. At many institutions this "core" subject has received the name of "educational biology," and it is hoped to develop it to the prominence that educational sociology and educational psychology have received in the education curriculum. Now so much of the time of the prospective teachers is devoted to methods courses, practice teaching, etc., that the content of most basis courses suffers. Thus educational biology

at the present time, despite the protests of many who teach it, is a one semester course. The administrative difficulties referred to prevent the giving of laboratory work in most cases, hence it is recommended that generous provision be made for demonstration and visualization.

As biologists, we are glad for the recognition of this function which biology may be made to serve, but we fear that the program is too ambitious under the conditions prescribed, especially since it appears to be the common experience of those who have taught both liberal arts and education students, as well as the supreme mentors in "education" themselves, that the latter group of students does not measure up mentally to the former group. Indeed, it is said on good authority that at least one investigation, whose publication was suppressed, showed that liberal arts trained teachers obtained quite as good results as those with specific training in methods from teachers' colleges in a certain state, a fact which might have had some influence on the appropriations granted the rapidly developing teachers' college system there. In last analysis, then, this latest fad course in biology would seem to raise anew, and in a time when the supply of teachers seems to be exceeding the demand, the old question of genuine standards among our brethren in "education" or the problem of methods vs. content, as expressed in the popular conception that a knowledge of teaching methods is an adequate substitute for wide knowledge of subject matter. The hopeful sign, however, is that the teachers' colleges, lately of a secondary level, show signs of early becoming vocational liberal arts colleges.

As regards the books listed, the first, so far as presenting an intellectual challenge is concerned, is scarcely better, if any, than some of the really good secondary texts on the market. Its emphasis is on physiology with a debatable minimum of anatomical detail. Only loose thinking will group a horseshoe crab in an illustration with a common crab under the title "crabs" together with the qualifying statement that it is not closely related to the common crab. More perniciously false is the statement that insulin cannot be administered by mouth, as every physician can testify. And this is biological *science*, and humanization of it with a vengeance!

The second, despite an occasional minor discrepancy, is of a decidedly high scholastic tone. The greater part of it is composed of materials which we would associate with courses in evolution, heredity, and eugenics, with really excellent teaching applications interspersed. Thus it is essentially the latter third of a liberal arts course in biology but without the antecedent preparation. While we appreciate the author's courage in thus assaulting the soft science situation prevalent in the teachers' colleges, we wonder how he can do justice to such materials with the background of the students, for the authors of the first text, teachers present or past in the same system, apologize for the nonchallenging character of their book by the statement that investigations indicate about one-half of those enrolled in teachers training courses have had no previous training in Biology!

After all, why not a good course in General Biology instead of this stuff, with teaching application, suggestions, and above all, humanisms as it goes along?

A CONTRIBUTION TO THE KNOWLEDGE OF FLORIDA ODONATA. *University of Florida Publication, Biological Science Series, Vol. I, No. 1.*

By C. Francis Byers. University Bookstore
\$1.00 Gainesville, Florida

5 $\frac{5}{8}$ x 9 $\frac{1}{8}$; 327 (paper)

This stout volume contributes the first of a special series of contributions from the Department of Biology of the University of Florida. It is an excellent account of the dragon flies of the state, treating first the taxonomy and then the ecology. One hundred and nineteen species are listed, and 114 described, the other five listed being dubious. Seventeen species were reared from nymphal instar stages to adults, seven of these furnishing new life histories. To the general biologist the ecological section will be the most interesting, with its accounts of habits and habitats. A penetrating discussion of distribution and migration leads to the conclusion that temperature is the most important single factor affecting the distribution of Odonata in Florida, acting as a barrier to their migration.



PUBLICATIONS OF THE UNIVERSITY OF OKLAHOMA BIOLOGICAL SURVEY, Vol. I, Nos. 1, 2, 3. Containing following articles: *Tentative Program of the Survey*, by A. Richards; *Notes on Oklahoma Fishes*, and *Oklahoma and Arkansas Fishes*, by Carl L. Hubbs and A. I. Ortenburger.

University of Oklahoma Press
\$1.00 Norman

6 x 9 $\frac{1}{2}$; 112 + 13 plates (paper)

An extensive survey of the State of Oklahoma should yield very interesting results. The area, besides being a meeting place for fauna and flora from the north and the south and from the east and the

west, contains regions of high and low rainfall, salt plains, high plateaus, extensive forested areas and grass lands. While a certain amount of field work has already been done by independent workers it is now planned to organize the work. An outline of the program is presented in this bulletin together with two papers on fishes of the state and neighboring regions.



PRAKTIKUM DER GEWEBEPFLEGE ODER EXPLANTATION BESONDERS DER GEWEBEZÜCHTUNG.

By Rhoda Erdmann. Julius Springer
14.80 marks Berlin

6 x 9 $\frac{1}{2}$; viii + 148 (paper)

The second edition, not greatly enlarged, but considerably rewritten and improved, of a useful treatise on the technique of tissue culture, with brief laboratory directions for a course in the subject.



HOLIDAY MEADOW.

By Edith M. Patch. The Macmillan Co.
\$2.00 7 $\frac{3}{8}$ x 8; 165 New York

This, a book for young children, is a charming and accurate introduction to animal and plant life as found in any meadow one might come upon during a short stroll. The illustrations are usually not well reproduced.



PRESSON BIOLOGY TEST. Test 1: Plant Biology. Test 2: Animal Biology. By John M. Presson, under the direction of LeRoy A. King. World Book Co.

Yonkers, N. Y.

Test 1 and Test 2 sold separately in packages of 25, \$1.20 per package

6 $\frac{1}{2}$ x 10; 52 (paper)

HUMAN BIOLOGY

HUMAN HISTORY.

By G. Elliot Smith.

W. W. Norton and Co., Inc.

\$5.00 5½ x 8½; xviii + 472 New York

The purpose of this book "is to search for the deep motives that have shaped Man's career, and to call attention to the vital factors in human thought and behaviour which have been ignored by most writers." The author is an authority on the comparative morphology of man and an eminent teacher of anatomy. This book will arouse much controversy among biologists and humanists. Whether it will bring about a cooperation of the biologists and the humanists towards a better understanding of human thought and action remains to be seen.

The chief aim of such a study should be, according to the author,

study of the actions of the organism as a whole, the behaviour of living men and women in all its puzzling manifestations. Moreover it should include something more than behaviour, in the sense of such actions as can be observed and recorded. The thoughts and feelings that provide the motives for men's behaviour are the things that matter most.

A great deal of credit for the distinctive character of civilization is given to the embalmer. The art of mummification developed out of the great urge to find a way to "prolong the existence of the body so that it might be reanimated as a living being." This created "not only many of the essential arts and crafts (architecture, stone and wood-working, sculpture and painting, the drama, dancing and music) that represent the scaffolding of civilisation, but also the deepest aspirations of the human spirit, the motives which have influenced the thoughts and actions of countless millions of human beings throughout the whole history of civilization." But many centuries before

the era of mummification man was "building up the fabric of civilisation under the influence of doctrines based upon his ideas of the functions of the heart and blood, the breath and moisture, the placenta and the hypothetical 'life-substance.'" Primitive man he believes to have been and still to be (as he is found in remote places today) "decent, generous and peaceful." However, early civilization, once under way, was concerned with building up a system whereby individuals were more or less subjected to the tyranny of a State System. A new era in the progress of civilization was ushered in in the sixth century B.C. when the Ionians broke down the heavy shackles which this system imposed on the great mass of people and men and women became free to "think and act without restraint." Since that time "human history has been a conflict between the rationalism of Hellas and the superstition of Egypt." To ancient Egypt he gives the credit of laying the foundation of civilization.

The book contains many illustrations, a brief bibliography and an index.



BULLETIN DER SCHWEIZERISCHEN
GESELLSCHAFT FÜR ANTHROPOLOGIE
UND ETHNOLOGIE. 1929/30.

6. Jahrgang.

By the Société Suisse d'Anthropologie et
d'Ethnologie. Büchler und Co.

6½ x 9; 32 (paper) Bern



THE IMMIGRANT WOMAN AND HER
JOB. *Bulletin of the Women's Bureau*, No. 74.
By Caroline Manning.

U. S. Government Printing Office
30 cents Washington

5½ x 9½; ix + 179 (paper)

A survey under the auspices of the

Woman's Bureau of the Department of Labor, to ascertain in what manner the immigrant woman is fitting into American industrial life. Over 2000 women were interviewed. Two regions were studied. Philadelphia with its large clothing and textile industries, besides numerous lesser trades, offers a wide variety of occupations for the immigrant woman. In the Lehigh River Valley, 50 miles to the north of Philadelphia, where originally were only steel and cement works, large cigar factories and silk mills have grown up since 1905, giving employment to great numbers of women. Austria and Hungary have furnished the larger part of the workers in the Lehigh Valley, while in Philadelphia Russians predominate.

The report is divided into three sections. The first "deals with the problems of the women in industrial employment, the second with the much smaller group occupied more casually in industrial home work, and the third with the women attending the beginners' English classes in the Philadelphia Public Evening Schools." A very adequate summary of the results is given in the last three pages of the report. In an appendix are given the schedule forms.



LA POPOLAZIONE DI TRIESTE (1875-1928).

By P. Luzzatto Fegiz.

Istituto Statistico-Economico

9½ x 13¼; 106

Trieste



THE MONEY VALUE OF A MAN.

By Louis I. Dublin and Alfred J. Lotka.

The Ronald Press Co.

\$5.00 5½ x 8½; xv. + 264 New York

The authors have applied Farr's method to modern American life tables and wage

scales in order to estimate the present worth of the gross and net future earnings of men of different ages and income classes. The book should be of great use in questions of compensation for injury or death. It is interesting to note the conclusion that the earning capacity of the population has increased rather than decreased as a result of the advance in the mean age of our population.



YOURSELF, INC. *The Story of the Human Body.*

By Adolph Elwyn.

Brentano's

\$3.50 5¼ x 8½; iv + 320 New York

The great popular success of Dr. Logan Clendenning's "The Human Body" seems to have stimulated the production of a host of similar treatises. The present volume is a clear, accurate and unsensational account for the general reader of the simpler elements of human anatomy, physiology, and hygiene. The book is a sound rather than brilliant performance. It is rather more sparingly illustrated than is usual in popular biological books. Its real field of usefulness seems to us likely to be found as a text for high school and small college classes in hygiene, rather than as entertainment for the general reader.



ANTARCTIC ADVENTURE AND RESEARCH.

By Griffith Taylor.

D. Appleton and Co.

\$2.00 5 x 7½; xi + 245 New York

Professor Taylor, himself geologist in Scott's last expedition, gives in this book a history of Antarctic exploration and a description of the geography, climate and resources of the Antarctic regions. Although it inevitably lacks some of the picturesque detail that enlivens narratives

of individual expeditions, it will serve as an admirable background. The book contains both bibliography and index.



YOUTH AND CRIME. *A Study of the Prevalence and Treatment of Delinquency Among Boys Over Juvenile-Court Age in Chicago.* United States Department of Labor, Children's Bureau Publication No. 196.

By Dorothy Williams Burke.

U. S. Government Printing Office
35 cents Washington

5 $\frac{3}{4}$ x 9 $\frac{1}{8}$; v + 205 (paper)

This is a study of the prevalence and treatment of delinquency among boys over juvenile-court age (17 to 20 years of age) in Chicago. Statistics covering the years 1915 to 1925 collected by the police department, the jail and the municipal court furnish the basis of the report. The first two sections deal with "General findings and recommendations" and "Methods of dealing with boy offenders in Chicago." The third section gives an analysis of a selected group of cases (972) dealt with by the boy's court branch of the municipal court, while the fourth and last gives a detailed study of 82 boys handled by the same court. In Appendix A is discussed the extent to which cases studied represent the entire group and in Appendix B the exclusion of certain cases.



OUTLINE OF JEWISH KNOWLEDGE, *being a History of the Jewish People and an Anthology of Jewish Literature from the Earliest Times to the Present; including a Brief Account of the History of Civilization of the Nations with Whom the Jews Have Come into Contact, and an Exposition of the Present-day Status and Problems of the Jewries of the World. In Twelve Volumes. Vol. I.*

Founding of the Nation. From the Earliest Times to the Death of Saul.

By Israel Goldberg and Samson Benderly.

Bureau of Jewish Education

\$2.00 5 $\frac{1}{2}$ x 8 $\frac{1}{2}$; xxviii + 382 New York

10% discount for 10-20 copies

20% discount for 20-50 copies

This is the first of a series of volumes intended to make Jewish history and literature better known to the younger generation of Jews. The authors follow the traditional account rather closely, with much the same slurring over of the more blood-thirsty aspects of the religion of the early Hebrews as is customary in Christian accounts of the Old Testament.



PROCEEDINGS OF THE THIRD RACE BETTERMENT CONFERENCE, JANUARY 2-6, 1928. *Under the Auspices of the Race Betterment Foundation, Battle Creek, Michigan.*

Race Betterment Foundation

\$5.00 (cloth)

Battle Creek

\$2.00 (paper)

6 x 9; xxx + 748

A collection of papers read by various authors, some of whom were men of science, on numerous aspects of eugenics, as well as other forms of the uplift, at a series of meetings at the Battle Creek Sanitarium, under the auspices of the Race Betterment Foundation, of which the president is stated to be Dr. John Harvey Kellogg.



THE BANTU TRIBES OF SOUTH AFRICA. *Reproductions of Photographic Studies. Vol. II, Section I, Plates I-XXVI. The Suto-Chuana Tribes. Sub-Group I, The Bechuana. With Introductory Articles on The Suto-Chuana Tribes and the Bechuana,*

by G. P. Lestrade, and *Descriptive Notes on the Plates.*

By A. M. Duggan-Cronin.

Deighton, Bell and Co., Ltd.

21 shillings Cambridge, Eng.

8½ x 11½; 23 + 26 plates (paper)

Section I of Volume II of this interesting and valuable anthropological study of the Bantu tribes contains an introductory chapter, a section on the Bechuana, and twenty-six excellent photographic plates with descriptive notes. A review of Section I, Volume I has been given in an earlier number of this journal.



SPECIAL REPORT ON CONTRIBUTORY CAUSES OF DEATH. 1926. Canada. Dominion Bureau of Statistics, Demography Branch.

F. A. Acland

Free 6½ x 9¾; 150 (paper) Ottawa

SPECIAL REPORT ON ORDER OF BIRTH OF CHILDREN BORN IN 1925. Canada. Dominion Bureau of Statistics, Demography Branch.

F. A. Acland

Free 6½ x 9¾; 49 (paper) Ottawa

The data on order of birth are tabulated by age of mother and occupation of father. The sizes of family for different occupations show much the same tendency as in other countries, the wives, aged 40-44 years, of professional workers having borne 4.67 children, while the wives in the same age-group of fishermen had borne 8.83 and those of coal miners 8.87 children.



UNDER HEAD-HUNTERS' EYES.

By A. C. Bowers.

The Judson Press

\$2.00 net 5 x 7½; 248 Philadelphia

The author of this book, having been a missionary for more than twenty-five years in Assam and Bengal, writes of the ideals

and outlook of these people as they have been revolutionized by the impact of Christianity. Naturally he has many interesting things to say, but his point of view is swayed by his desire to show that "the idealism of Christ is already bearing fruit in giving healing and peace to many."



THE IMMIGRATION WORK OF THE DEPARTMENT OF STATE AND ITS CONSULAR OFFICERS. *Department of State Publication No. 22.*

U. S. Government Printing Office

10 cents

Washington

5¼ x 9½; iii + 49 (paper)

A statistical account of the work of the Department of State in administering the Immigration Act.



CARE OF AGED PERSONS IN THE UNITED STATES. *Bulletin of the United States Bureau of Labor Statistics No. 489.*

U. S. Government Printing Office

70 cents

Washington

5¼ x 9½; vi + 305 (paper)

A study of pension plans, old people's homes, and almshouses.



BIRTH AND DEATH RATES OF THE FEEBLE MINDED. *Eugenics Record Office Bulletin No. 26.*

By Charles V. Green. *Eugenics Record Office*

25 cents Cold Spring Harbor, Long Island

6 x 9; 34 (paper)

The author finds that the birth-rate among the feeble-minded is high and that the number of offspring much more than replaces the probable parental group.

LEARNING AND GROWTH IN IDENTICAL INFANT TWINS. *An Experimental Study of the Method of Co-Twin Control. Genetic Psychology Monographs Vol. VI, No. 1.*

By *Arnold Gesell and Helen Thompson.*

Clark University Press

\$2.00

Worcester, Mass.

6½ x 9½; 124 (paper)

This interesting study of a pair of identical twins during the first year and a half of their lives leads to the general conclusion that the preponderant influence in the determination of infant behavior pattern is the maturation of the neural structures. "There is no conclusive evidence that practice and exercise even hasten the actual appearance of types of reaction like climbing and tower building." One of the twins was trained and the other kept as control without training. At age 50 weeks after four weeks of training twin T climbed an experimental staircase "with avidity and without assistance." At 52 weeks she climbed the staircase in 26 seconds. But twin C, without any previous training whatever, climbed the same staircase unaided at 53 weeks in 45 seconds.



THE PEOPLING OF AUSTRALIA.

By *W. E. Agar, Henry Barkley, H. Benham, J. B. Brigden, A. H. Charteris, H. W. Cilento, J. Lyng, E. T. McPhee, P. D. Phillips, C. H. Wickens, G. L. Wood.* Edited by *P. D. Phillips and G. L. Wood.* With a Foreword by *J. G. Latham.*

The Macmillan Co.

\$2.50 4½ x 7½; xi + 300

New York

A collection of eleven articles, some of which have already appeared elsewhere. The authors are all Australians, either university lecturers and professors or public

servants whose work has a direct bearing on the problems which are confronting Australia at the present day in regard to its development. Such problems are discussed as the absorptive capacity of the continent for population, the optimum size of population, urbanization, white settlements in tropical Australia, general quality of the population, immigration policy, climatic factors affecting the distribution of peoples, etc. Australia's present population is placed at 6 millions. It is something over 140 years ago that the first white settlement was made on the continent. It has been estimated that at that time the number of natives probably did not exceed 150,000. To-day the number is hardly more than 60,000. Of the present population 98 per cent are British subjects by birth, 1.3 are black, 0.45 yellow and 0.25 brown. Concerning the racial constitution of the Australians it is estimated that 82 per cent of the white population is Nordic, 13 per cent Mediterranean and 5 per cent Alpine. Under the Immigration Restriction Act quotas have already been established.



HUMAN BIOLOGY AND RACIAL WELFARE.

Contributors: *Walter B. Cannon, Alexis Carrel, Edmund V. Cowdry, Edwin G. Conklin, Charles B. Davenport, John Dewey, Haven Emerson, John F. Fulton, William K. Gregory, William Healy, Ales Hrdlicka, Ellsworth Huntington, Paul A. Lewis, Archibald B. Macallum, Elmer V. McCollum, Robert A. Millikan, George H. Parker, Harry A. Overstreet, Raymond Pearl, Earle B. Phelps, Sir Humphrey Rolleston, Henry N. Russell, Sir Chas. S. Sherrington, William M. Wheeler, Clark Wissler, Robert M. Yerkes, Hans Zinsser.*

Edited by Edmund V. Cowdry, with an Introduction by Edwin R. Embree.

Paul B. Hoeber, Inc.

\$6.00 net $5\frac{1}{2} \times 9\frac{1}{2}$; xviii + 612 New York

This volume, with its distinguished list of contributors, is intended for students about to specialize, and for mature readers who wish to learn something of what is now known about the human animal. The chapters are naturally somewhat uneven in quality, but there is good and interesting reading in a large number of them. The second part of the title might lead one to expect a good deal of uplift, an expectation hardly realized. Most of the contributors dodge the uplift, and even the last two chapters, "The Purposive Improvement of the Human Race" (Conklin) and "The Intentional Shaping of Human Opinion" (Overstreet) are singularly moderate in the hopes they hold out for any improvement of the race. There are short reference lists for the different chapters, and an index.



ZOOLOGY

THE BOOK OF BIRD LIFE. *A Study of Birds in Their Native Haunts; with Photographs by the Author.*

By Arthur A. Allen.

D. Van Nostrand Co., Inc.

\$3.50 6×9 ; xix + 426 New York

Bird lovers and amateur naturalists will find this book delightful reading. It is in no sense a manual. Rather has the author sought to introduce the bird to the reader as a living animal. The first part deals with "the laws that govern the occurrence of birds in any locality; their relation to the environment and to each other; the principles underlying song, courtship, nesting, and other habits; the

nature of the many nice adaptations of structure, and the explanation of the varied colors of birds together with the relations of birds to man." The second part deals with methods of studying the bird in its environment. The book contains many excellent illustrations showing the bird in its natural environment; lists of suggested readings are given, there is a chapter on "Suggestions for the intensive study of a species" and an index.



IN THE ZOO. *Representing Twenty-Seven years of Observation and Study of the Animals in the New York Zoological Park.*

By W. Reid Blair. Foreword by Madison Grant. Photographically Illustrated by Elwin R. Sanborn. Charles Scribner's Sons
\$2.50 $5\frac{3}{4} \times 8$; xii + 195 New York

In this book the Director of the New York Zoological Park tells how his charges are cared for, how they are fed, and how medical, surgical and dental treatment is administered to them. The book is amusingly written and well illustrated. Although it is intended primarily for the general reader, much of it, especially the medical and surgical portion, will be of interest to the professional biologist.



LABORATORY EXERCISES IN ZOOLOGY. *A Practical Student's Manual for Classes in Animal Biology.*

By William M. Barrows. World Book Co.
84 cents Yonkers-on-Hudson, N. Y.

$5\frac{3}{8} \times 8$; vi + 103

This excellent laboratory manual deals largely with living forms. A useful book to place in the hands of students of elementary biology.

THE GALL WASP GENUS CYNIPS.

A Study in the Origin of Species. Waterman Institute for Scientific Research Publication No. 42; Contribution from the Department of Zoölogy, Indiana University, No. 220 (Entomological Series No. 7).

By Alfred C. Kinsey.

Indiana University Bookstore

\$2.50 (paper) 5 $\frac{3}{4}$ x 9; 577 Bloomington
\$3.00 (cloth)

The author of this intensive study of the genus *Cynips* has performed the arduous task of examining over 17,000 insects and 54,000 galls. The larger part of the book, Part II, is taken up with systematic data, illustrations, key, etc. Part I is devoted to a discussion of the bearing which the results of this investigation have upon the problems pertaining to the origin of species. The author finds that mutations in *Cynips* "have been the chief source of new species, but only when they are isolated from close relatives with which they might have interbred. Autho hybrid individuals prove common, and local colonies which have arisen by hybridization between related species are not unknown, the isolation of such hybrid populations to form species seems to have occurred in only a few instances in this genus." A taxonomic revision of the genus has been made. As redefined the group is a "homogeneous unit delimited by insect morphology, gall characters, host relationships, life histories, and geographic distribution." Of the 93 species in the group 45 have been previously described, and 48 are new. Six cases of alternation of generations have been added to the five already recorded.

The book is well illustrated with distribution maps and figures of the insects studied—something over 400 in all. There is a bibliography pertaining to the general biological discussion in Part I, and an index.

AQUATIC MAMMALS. *Their Adaptations to Life in the Water.*

By A. Brazier Howell. Charles C. Thomas
\$5.00 postpaid Springfield, Ill.

6 x 8 $\frac{3}{4}$; xii + 338

In this book Dr. Howell considers the many remarkable adaptations of aquatic mammals to their life in the water. Being designed for a wider public than the anatomists and mammalogists, the book is written "in an essentially nontechnical manner." There is, however, no attempt to jazz up the subject. There is a bibliography and an index.



REPORT OF THE UNITED STATES COMMISSIONER OF FISHERIES for the Fiscal Year 1928, with Appendixes. Part II.

U. S. Government Printing Office
\$1.65 5 $\frac{3}{4}$ x 9; iv + 670 Washington

This part of the report consists of the *Check List of the Fishes and Fishlike Vertebrates of North and Middle America North of the Northern Boundary of Venezuela and Colombia*, by David Starr Jordan, Barton Warren Evermann, and Howard Walton Clark, a revision of Jordan and Evermann's Check List of 1896. The number of species enumerated has increased from 3,100 to 4,139. There are indexes of common and scientific names. In the interesting but brief discussion of the origin of species the authors conclude that "it does not appear that any species of fishes have arisen by mutation or from hybridization, though the latter possibility is greater than the former."



DIE TIERWELT DER NORD- UND OSTSEE. Lieferung XVI. Lieferung XVII. Edited by G. Grimpe and E. Wagler. Akademische Verlagsgesellschaft m.b.H.

Lief. XVI, 21 marks

Lief. XVII, 13.50 marks

6 x 8½; 244 (paper)

158 (paper)

These two parts of this valuable work, previous numbers of which have been noted in these columns, deal with the following groups: *Rotatoria*, by A. Remane; *Ostracoda*, by W. Klie; *halophilic and halobiontic Coleoptera*, by H. v. Lengerken; *Peridinia*, by N. Peters; *Scyphozoa*, by Th. Krumbach.



A CONSPECTUS OF THE MARINE AND FRESH-WATER CILIATA BELONGING TO THE SUBORDER TINTINNOINEA, WITH DESCRIPTIONS OF NEW SPECIES PRINCIPALLY FROM THE AGASSIZ EXPEDITION TO THE EASTERN TROPICAL PACIFIC 1904-1905. *University of California Publications in Zoology, Vol. 34.*

By Charles A. Kofoid and Arthur S. Campbell.

University of California Press

\$5.00 7 x 10½; 403 Berkeley

This report is based upon material from the eastern part of the Pacific Ocean including the north temperate, tropical and south temperate regions. The collections were made by the Agassiz expedition of 1904-1905, various expeditions of the U.S.S. Albatross, as well as by individual members of the Scripps Institution and the University of California. This particular protozoan group is treated as a whole. It includes 51 genera, including 23 which are new. There are listed 276 new species while 38 others are given new names. Figures of all the species are included in the text, there is a lengthy literature list and a detailed index.

Leipzig

RECORDS OF CHANGES IN COLOR AMONG FISHES. *Zoologica, Vol. IX, No. 9.*

By Charles H. Townsend.

New York Zoological Society\$1.85 *Zoological Park, N. Y. City*

6½ x 9½; 58 (paper)

In this beautifully illustrated article the Director of the New York Aquarium records the color phases of the tropical fishes in the Aquarium.



THE FRESH WATER MOLLUSCA OF WISCONSIN. *Part I. Gastropoda. Part II. Pelecypoda.*

By Frank C. Baker.

Wisconsin Academy of Sciences, Arts, and Letters

\$3.00 Madison

Part I. 6½ x 9½; xx + 507 + 28 plates

\$3.00

Part II. 6½ x 9½; vi + 495 + 77 plates (paper)

In this excellent monograph "the account of each species is given under several headings, including the shell, animal, parts of its anatomy (genitalia, jaw, radula), its ecology, its distribution by drainage systems in the State and remarks concerning the chief features of its variation, value, or general interest." There is a bibliography of 23 pages, a glossary and an index. Mr. Baker agrees with Coe that the "environment permits and directs evolution but does not cause it."



BOTANY

THE PENICILLIA.

By Charles Thom. With the assistance of Margaret B. Church, O. E. May and M. A.

Raines. *The Williams and Wilkins Co.*
\$10.00 5 $\frac{7}{8}$ x 9; xiii + 644 Baltimore

A highly important contribution to the literature of mycology. The molds of *Penicillia* cause widespread depredation throughout the world. They rot fruit, vegetables and meat; discolor fibers, wood, paper stock and stored paper; grain in storage is frequently injured by them, and they contaminate laboratory cultures, soft drinks and bottled waters. The best that can be said of them is that they produce Camembert and Roquefort cheese. But in addition to all the havoc which they work, for the investigator they have an added sin: they are extremely difficult to classify. The author of this book has devoted many years in an endeavor to disentangle this problem. Ultimately he based his classification on "delimitation of groups presenting common morphological and cultural characters." Concerning the difficulties which *Penicillia* present, he says,

Alive and actually growing, they have individuality as pronounced as their capabilities for evil, but the elements of that individuality, color, odor, and habit of growth, are as evanescent as frost designs on a window pane in winter. To lay a foundation for a permanent knowledge of this lot of molds, the whole range of morphology and physiology must be searched for marks of separation stable enough, and sharply enough marked to convey to the reader a definite picture of the organisms studied. Then organism by organism they must be fitted into the scheme of classification to form a consistent and interpretable whole.

The work falls into two sections. The first ten chapters are devoted to a discussion of the problems, activities, and uses of the organism. The remaining seventeen are taxonomic. There are numerous illustrations, a lengthy bibliography, a general index and an index to species.

PLANT COMPETITION. *An Analysis of Community Functions. Carnegie Institution of Washington Publication No. 398.*

By Frederic E. Clements, John E. Weaver and Herbert C. Hanson. *Carnegie Institution of Washington, D. C.*
\$3.25 (paper)
\$4.25 (cloth)

6 $\frac{3}{4}$ x 10; xvi + 340

This important monograph is the second in a series dealing with the functions of the plant community as a complex organism. The first, "Experimental Vegetation," appeared in 1924. It is the plan of the authors to prepare other volumes dealing with reaction, coaction, adaptation, and migration and invasion. The studies on competition and reaction reported in the present volume have been made under both natural and controlled conditions "involving the utilization of climax and seral communities in nature, field crops and greenhouse control." The first chapter deals with a "History of the competition concept;" then follow sections on "Transplant cultures in sub-climax prairie," "Transplant cultures in true prairie," "Supplementary studies of competition in the prairie," "Competition in the ecotone between woodland and prairie," "Competition in cultivated fields," "The relative importance of the factors in competition" and "Functional studies in control cultures." The work is excellently illustrated with many figures and photographic reproductions, and contains 132 tables exhibiting growth, analyses, etc. There is a lengthy bibliography.



FLORA OF THE HERMIT SHALE, GRAND CANYON, ARIZONA. *Carnegie Institution of Washington Publication No. 405.*

By David White. Carnegie Institution of
\$2.50 (paper) Washington, D. C.
\$3.50 (cloth)

6 $\frac{1}{2}$ x 10; 221

The first section of this study is devoted to a description of the geological environment, the second, to the composition, age and relations and the third, to the description of the Hermit flora. The flora points to a semi-arid climate with a long dry season during the Hermit time. Altogether 34 species of fossil plants are described. Insect wings were found, numerous foot prints of vertebrates and three fossil forms which are probably of animal origin. The investigator expects further study to yield many more species of plants. The photographic plates, of which there are 51, are remarkably fine.



BIBLIOTHECA BOTANICA. Heft 99.
*Geschichte und Geographie der Veronica-Gruppe
Megasperma.*

By Ernst Lehmann.

E. Schweizerbart'sche Verlagsbuchhandlung
19 marks Stuttgart

9 x 12 $\frac{1}{2}$; 55 + 1 table (paper)

An interesting exposition of the problems of speciation which are presented by the European species of the genus *Veronica*, the common "speedwell." The facts regarding the history of the genus and the geographical distribution of the species in the *Megasperma* group are well presented, and they clearly demonstrate that the geneticist has here a fine opportunity to try his hand at unravelling an exceedingly puzzling problem of evolution. Why is it that, in spite of the ubiquitous occurrence of the weed, and its great facilities for dispersion, there exist well marked, and clearly differentiated geographical varieties, in some cases even overlapping in their ranges?

PLANT BIOLOGY. *An Outline of the
Principles Underlying Plant Activity and
Structure.*

By H. Godwin.

University Press

8s. 6d.

Cambridge

\$2.90

The Macmillan Co.

New York

5 $\frac{1}{2}$ x 7 $\frac{1}{2}$; x + 265

A text book for first-year medical and biological students. Especial emphasis is laid on the physiological point of view and a consideration of the simpler characters of the physicochemical background of plant life. The book is well illustrated and indexed.



BACTERIAL METABOLISM.

By Marjory Stephenson.

Longmans, Green and Co.

\$7.00 6 x 9 $\frac{1}{8}$; xi + 320 New York

This book belongs to the excellent series of monographs on biochemistry, edited by R. H. A. Plimmer and Sir F. G. Hopkins. In the present treatise the author's aim is to present facts which will lead to an understanding of "bacteria as living organisms apart from their rôle as disease germs or the bearer of commercially important catalysts." Although Miss Stephenson considers that she has doubtless included material which later may prove irrelevant to the subject, as well as omitted important facts, her book shows that she has made an extraordinarily careful and discriminating study of the physiology of bacteria. In the text are 83 tables. There is an appendix on the "Barcroft Differential Manometer" and a bibliography of about 800 titles. The book is well indexed.



VEGETATIVE PROPAGATION FROM
THE STANDPOINT OF PLANT ANAT-

OMY. U. S. Department of Agriculture
Technical Bulletin No. 151

By J. H. Priestley and Charles F. Swingle.

U. S. Government Printing Office

35 cents

Washington

5 $\frac{3}{4}$ x 9 $\frac{1}{8}$; 99 + 24 plates (paper)

A report of a technical study of vegetative propagation, primarily of the internal factors involved, made for the purpose of obtaining a better understanding of those plants which offer more or less difficulty in propagation by this method. The work has been limited to a study of the phenomenon as it occurs in the flowering plants, usually in the dicotyledons. A detailed analysis of the anatomical basis of vegetative propagation is given. Numerous illustrations are included in the text and a literature list of 190 titles is given.



BERGEY'S MANUAL OF DETERMINATIVE BACTERIOLOGY. *A Key for the Identification of Organisms of the Class Schizomycetes. Third Edition.*

By David H. Bergey. Assisted by a Committee of the Society of American Bacteriologists, Francis C. Harrison, Robert S. Breed, Bernard W. Hammer, Frank M. Huntoon, with an Index by Robert S. Breed.

The Williams and Wilkins Co.

\$6.00 5 $\frac{3}{4}$ x 9; xviii + 589 Baltimore

The third edition of this standard manual, which is indeed virtually indispensable for any bacteriologist, has been greatly enlarged, and rather extensively revised. Over 200 additional organisms are included, two new tribes are recognized, as well as several new genera. A solid useful piece of work.



GROWTH AND TROPIC MOVEMENT OF PLANTS.

By Sir Jagadis Chunder Bose.

Longmans, Green and Co.

New York

\$8.40

5 $\frac{1}{2}$ x 8 $\frac{1}{2}$; xxix + 447

This volume is the continuation and, according to the publisher's statement the completion, of the distinguished author's investigations of the movements of plants. A wide range of subjects is discussed, the data being obtained by the use of the author's automatic high magnification crescograph, and various modifications of it. The general conclusion is:

The fundamental principle is that growth is retarded by strong and accelerated by weak stimulation of whatever kind. Closely connected with it is the further principle that direct stimulation retards and indirect stimulation accelerates the rate of growth: this is the essential feature of the mechanism of tropisms. There is no longer any ground for assuming distinct irritabilities, such as the phototropic and the geotropic, or negative and positive phototropism and geotropism: these terms may remain as merely descriptive of the visible response. There is but one irritability of the growing organ which responds to all stimuli that may act upon it, and in essentially the same manner.

This, like many of Dr. Bose's books, is perhaps quite as interesting from the standpoint of the philosophy of scientific methodology as for its biological results. There is presented to the reader a series of separate single experiments, from each of which single experiments a principle or law is deduced, some of extremely far reaching significance. Doubtless Dr. Bose actually performed *many* experiments like each one of the single ones he presents to the reader. Also, doubtless (unless all other biologists are working in a state of profound delusion) there was more or less *variation* in the results of a set of repeated experiments of the same kind. But of variation and divergences in the results of repeated experiments, which are, to the author's great pride and satisfaction, of a more precise and delicate quantitative character than almost any other biological

experiments ever made, Dr. Bose says never a word except to suggest occasionally that if divergences from the stated result should occur they would be due to errors of technique. Perhaps it is this seventeenth century rationalistic attitude, with its unquestioning trust in the crucial experiment carefully measured, and its correlative naïve neglect of differences, variations, and divergences, which has, in part, brought it about that plant physiologists generally appear not to accept Dr. Bose's results with anything approaching ardent enthusiasm.

On the other hand, it must be said that there are not a few present day biologists whose philosophical *summum bonum* is seventeenth century rationalism, pure and undefiled, though doubtless some of them would dislike to have their attitude so roughly characterized. To them Dr. Bose's work must, or at least ought to, seem good. There is probably a sweet satisfaction derivable from a real privy with God in His ability to "understand" natural phenomena.

In any case all biologists cannot but admire the extremely delicate and precise mensurational technique which Dr. Bose has brought to the service of biology.



MORPHOLOGY

LABORATORY GUIDE TO VERTEBRATE DISSECTION *for Students of Anatomy.*

By A. B. Appleton. The Macmillan Co.
\$6.50 New York

4 $\frac{3}{4}$ x 7 $\frac{1}{4}$; xix + 152

A guide to practical comparative anatomy which has been in use for several years in the University of Cambridge. The types dealt with are the lamprey, the dogfish, *Necturus*, the lizard, and the dog.

DIE FOSSILEN GEHIRNE.

By Tilly Edinger. Julius Springer
36 marks 6 $\frac{3}{8}$ x 9 $\frac{1}{2}$; 249 Berlin

In this thorough treatise on endocranial casts are collected the known data by classes and orders of the vertebrates. The author is critical of Marsh's "general law of brain growth." There is an annotated bibliography and an index.



WIE SOLLEN WIR ELITEGEHIRNE VERARBEITEN?

By C. v. Economo. Julius Springer
6.90 marks 6 $\frac{3}{8}$ x 9 $\frac{1}{2}$; 87 (paper) Berlin

A description of technique for the measurement and histological examination of the brain.



PHYSIOLOGY AND PATHOLOGY

ANTIVIRUSTHÉRAPIE. *Applications à l'Ophthalmologie, l'Oto-Rhino-Laryngologie, la Stomatologie, l'Entérologie, l'Urologie, la Gynécologie et l'Obstétrique, la Dermatologie, la Chirurgie, la Médecine Vétérinaire, la Sérothérapie Locale.*

By A. Besredka. Masson et Cie
40 francs Paris

5 $\frac{3}{8}$ x 9; viii + 430 (paper)

The use of vaccines for the cure of disease has been largely disappointing. Now comes Besredka to tell us that the reason is that in all cases we have been injecting the vaccines subcutaneously when actually we should have been applying them to the particular tissue the resistance of which we wished to raise. Thus, if we wish to cure boils we should inject the vaccine into the skin and if we wish to cure an enteritis we should give vaccines and bacterial filtrates by mouth. Besredka describes a number of ways in which

vaccines and what he calls antiviruses can be made. Pasteur showed that when bacteria are grown in a culture medium substances are produced which are inimical to further growth. Besredka obtains these substances in more concentrated form by filtering out the bacteria and then seeding the medium again. The antivirus so produced can then be used to combat the growth of bacteria in the body.

The present volume summarizes the reports of many investigators who claim to have obtained good results with the help of the new methods of vaccination. One hopes that it is all true; the theory is an attractive one and certainly the experiments should be carefully repeated. Unfortunately so many in the past have cried, "Eureka," that Besredka cannot complain if many of his readers refuse immediately to believe and to get excited. It is to be hoped that many will read this book, that some will repeat the experiments, and that they will then report their results.



MAGICIAN AND LEECH. *A Study in the Beginnings of Medicine with Special Reference to Ancient Egypt.*

By Warren R. Dawson.

Methuen and Co., Ltd.

7s. 6d. net

London

4 $\frac{3}{4}$ x 7 $\frac{1}{2}$; xiii + 159

The author of this interesting book has gone to the original medical documents for his material. He gives only a brief summary of what he has gleaned from the study of numerous papyri but it is a progressive picture of the evolution of medicine from early magic. In the course of time some of the early magicians perceived the wisdom of increasing their repertoire. Doses of substances were administered internally as well as externally along with the magic. The more effica-

cious of these doses naturally tended to survive their more fantastic fellows and eventually there were healers who confined themselves entirely to the practice of administering "medicines." Even so far back as the Pyramids there was the title of "Royal Physician—interpreter of a difficult science." The magician, however, was never driven out of business. Of special interest are the chapters on "The first medical books" and "Drugs and doses." We find as an ointment for a troublesome scalp the following: "Fat of a lion, 1 (part); fat of a hippopotamus, 1; fat of a crocodile, 1; fat of a cat, 1; fat of a snake, 1; fat of an ibex, 1. Mix into one mass; anoint the head therewith." Animals whole or in part played an important place in Egyptian prescriptions, the gall of animals being especially fancied as a medicine. The number of vegetable drugs was very large and we find castor oil a great favorite. Over 2000 prescriptions occur in the medical papyri of Pharaonic times.

Much time has been devoted by the author to the study of mummification. He believes that its importance in the development of medicine can hardly be overestimated, not only because of the knowledge which the early Egyptians acquired of human anatomy but because "it familiarized the popular mind for over twenty centuries with the idea of cutting the dead human body." This fact made it possible for the "Greek physicians of the Ptolemaic age to begin, for the first time, the systematic dissection of the human body, which popular prejudice forbade in all other parts of the world."



LES ÉRYTHRÉMIES DE L'ALTITUDE.
*Leurs Rapports avec la Maladie de Vaquez.
Étude Physiologique et Pathologique.*

By Carlos Monge.

22 francs

Masson et Cie

Paris

6 $\frac{3}{4}$ x 10; xi + 135 (paper)

If there is one place in the world in which the diseases due to living at high altitudes could be studied it should be Peru, and Dr. Monge is Professor of Internal Pathology at the University of Lima. There have been a number of scientific expeditions to the Alps, Pike's Peak, Peru, and the Sierras of California to study the changes which take place during the acclimation of individuals to high altitudes, but here is a book which deals more particularly with the chronic disturbances which appear in persons who live for years in the mountains. The main thesis of Dr. Monge is that in certain persons there is an insufficiency in the permeability of the lung to oxygen, an insufficiency which makes it difficult or impossible for them to become acclimated. He believes that mountain sickness is an acute form of erythremia. He describes also two chronic forms, one of which closely resembles Vaquez' disease. The book should be of great interest to all those who are concerned with the problems of respiration.



THE OCCULT CAUSES OF DISEASE.

Being a Compendium of the Teaching Laid Down in His "Volumen Paramirum" by Bombastus von Hohenheim, Better Known as Paracelsus.

By E. Wolfram

Rider and Co.

(done into English by Agnes Blake).

6 shillings 4 $\frac{1}{2}$ x 7 $\frac{3}{8}$; 296 London

Herr Wolfram interprets the doctrines of Paracelsus as being a form of Rosicrucianism. But is there any good evidence that Rosicrucianism existed before the seventeenth century? The book might serve as a storehouse of fallacies for a class

in logic to cut their teeth on. Thus cholera and arsenic poisoning are identified with each other because of the similarity of their symptoms. After reading the book we are still of the opinion that the importance of Paracelsus lies not in his occultism but in his turning from authority to the first-hand study of nature.



LES ACROCYANOSSES. *Troubles Vasculaires Cutanés d'Origine Nerveuse, Végétatif ou Centrale.*

By Fernand Layani.

Masson et Cie

32 francs 6 $\frac{1}{2}$ x 9 $\frac{1}{2}$; iv + 282 (paper) Paris

A syndrome is described which consists of cyanosis, generally of the extremities, associated with coldness of the parts affected, and secretory and trophic disturbances which never go so far as to produce gangrene. The author feels that this disease can be differentiated from those which now go by the names of Raynaud and Buerger. He believes that the primary disturbance is probably in the endocrine system and he attempts to cure it by giving to the patients extracts of the various glands of internal secretion. There is a good review of the European literature on the subject but, unfortunately, the author does not seem to have been aware of the recent work of George Brown and other Americans. The book should be of great interest to all those who deal with this problem of vascular spasm.



THE CANCER PROCESS. *An Examination of the Factors which Induce New Growth.*

By J. J. M. Shaw. E. and S. Livingstone

1 shilling net

Edinburgh

5 $\frac{1}{2}$ x 9; 16 (paper)

In the form of a brief, essentially dogmatic, statement without documentation

or systematic presentation of evidence, the author develops the thesis that "*Cancer is caused by prolonged contact between the cells of living tissue and any substance which possesses these three properties: VISCOSITY, INSOLUBILITY in tissue fluids, and TOXICITY to cell life.*" These three properties are found in concomitance in every substance which is capable of producing the cancer cell. Be it tar or stale sebaceous matter, shale oil or foul sputum, ethereal extract of tobacco or effete muco-pus, paraffin, applied and injected, or the cholesterin, lecithin, and fibrin of old extravasated blood, the trio of properties is always exhibited." The reasoning is well-knit and in some degree persuasive, but probably not quite adequate to support the heavy burden of so wide a generalization.



LEPROSY. *Survey Made in Forty Countries (1924-1927).*

By H. C. de Souza-Araujo.

Oswaldo Cruz Institute

\$4.00

Rio de Janeiro

7½ x 11½; 400 (paper)

(May be obtained from D. Appleton, New York; W. B. Saunders Co., Philadelphia; Cassel and Co., London; Masson et Cie, Paris; The Macmillan Co. of Canada, Toronto.)

(The total revenue of the Portuguese and English issues is reserved to form the fund of the Societas Internationalis Leprologiae, of Bergen, Norway.)

This monograph will interest many people. Physicians, hygienists, all who are concerned with making laws governing leper colonies as well as workers among the lepers will find it invaluable as a source book. The extent of the material presented is indicative of the labor and care which the author has expended in

making the survey. The work includes 66 tables dealing with statistics and numerous illustrations. At the conclusion of each section a bibliography is given of the literature which has appeared concerning leprosy in that particular country.



THE PHYSIOLOGY OF ORAL HYGIENE AND RECENT RESEARCH. *With Special Reference to Accessory Food Factors and the Incidence of Dental Caries.* By J. Sim Wallace.

Baillière, Tindall and Cox

10s. 6d. net 5½ x 8½; vii + 228 London

A collection of papers and addresses giving Dr. Wallace's reasons for concluding that dental caries is caused by the acid fermentation of carbohydrates and not by lack of vitamin D.



HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 311.*

Containing following articles: *Methoden zur Messung der Oberflächenspannung*, by A. Gyemant; *Methoden zur Bestimmung des elektrischen Widerstandes*, by Marie Wreschner; *Die Potentiometrie*, by E. Mislowitz.

Urban und Schwarzenberg

6 marks 7 x 10; 107 (paper) Berlin

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 323. Photochemische Arbeitsmethoden im Dienste der Biologie.*

By Ivan Plotnikow.

Urban und Schwarzenberg

13 marks 7 x 10; 260 (paper) Berlin

These two numbers of the Abderhalden *Handbuch* maintain the high standard of the work as a whole. The second of them, dealing with photochemical methods, will be particularly useful for its thorough discussion of light filters, and the technique of photometry.

BIOCHEMISTRY

OXIDATION-REDUCTION POTENTIALS.

By L. Michaelis. Translated from the German Manuscript by Louis B. Flexner.
J. B. Lippincott Co.
\$3.00 Philadelphia

5 $\frac{1}{4}$ x 8; xiii + 199

This monograph, by a distinguished worker on problems of hydrogen ion concentration and oxidation-reduction potential, will be useful to the biochemist.



DIE KOLLOIDE IN BIOLOGIE UND MEDIZIN.

By H. Bechhold. Theodor Steinkopff
32 marks (paper) Dresden
35 marks (bound)

6 $\frac{1}{4}$ x 9; xii + 586

This fifth edition of a standard treatise on colloids for biologists has been practically completely rewritten and greatly enlarged. It is abundantly and well illustrated, meticulously documented, and well indexed. The subject is treated under four general heads: I. Introduction to colloid research; II. Biocolloids; III. The organism as colloid system; IV. Toxicology, pharmacology, therapeutics, and microscopical technique. It is an excellent book.



HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 315*. Containing following articles: *Gasometrische Mikro-Kjeldahl-Stickstoffbestimmung*, by Donald D. van Slyke; *Methoden zur Untersuchung des Stoffwechsels von Leukocyten und*

Thrombocyten, by Walter Fleischmann; *Praktisches Verfahren bei Ernährungsversuchen*, by Arthur H. Smith and Lafayette B. Mendel.

Urban und Schwarzenberg
5 marks 7 x 10; 92 (paper) Berlin
HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 317*. *Fermentforschung*. Containing following articles: *Spezifische Nucleasen*, by Fr. Chrometzka and A. Schittenhelm; *Bestimmung von Harnstoff durch gasometrische Messung des durch die Einwirkung von Urease gebildeten Kohlendioxydes*, by Donald D. van Slyke; *Myrosinase*, by Fritz Wrede; *Chlorophyllase*, by Richard Willstätter; *Phosphatasen*, by Heinrich Lüers; *Gewinnung von proteolytisch einheitlichem Trypsin und Erepsin aus Pankreas und Darm*, by Ernst Waldschmidt-Leitz; *Trennung der Hefepro- teasen*, by W. Grassmann; *Über Luciferase von leuchtenden Tieren*, by E. Newton Harvey.

Urban und Schwarzenberg
8 marks 7 x 10; 143 (paper) Berlin
HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 322*. Containing following articles: *Methoden zur Untersuchung des Energieumsatzes in Muskeln und Nerven*, by J. L. Parkinson; *Die Arbeitsmaschine Johanssons*, by Ernst Abramson.

Urban und Schwarzenberg
7 marks 7 x 10; 116 (paper) Berlin
These three numbers of the Abderhalden *Handbuch* of biological technique deal with various biochemical procedure, as indicated by the titles. The article by Smith and Mendel in *Lief.* 315 will be found useful by many workers for the large number of experimental diets for specific purposes which it contains. The interest of the other articles in these three *Lieferungen* is mainly special to the biochemist and physiologist.

MIKROMETHODIK. *Quantitative Bestimmung der Harn-, Blut- und Organbestandteile in kleinen Mengen für klinische und experimentelle Zwecke.*

By Ludwig Pincussen.

Georg Thieme

7.50 marks

Leipzig

5 $\frac{1}{4}$ x 7 $\frac{3}{4}$; 225 (paper)

The fifth revised and enlarged edition of a standard guide to microchemical technique. An index has also been added.



SEX

THREE CONTRIBUTIONS TO THE THEORY OF SEX. *Fourth Edition. Nervous and Mental Disease Monograph Series No. 7.*

By Sigmund Freud (*Authorized translation by A. A. Brill*).

Nervous and Mental Disease Publishing Co.
\$2.50 New York and Washington

6 x 9; xiv + 104

Rereading this reprint of a pioneer treatise, which has become a classic in the course of the twenty odd years since it first appeared, leaves one with two outstanding and vivid impressions; first, that Freud has made an enormous and profound contribution to an understanding of the meaning of sex. Second, that his grasp and penetration of the workings of the human mind make the academic psychologists look silly, with their petty and precious tiddlings-about in the laboratory striving to measure things, without the faintest apparent understanding of the subtlety, the complexity, the integrated manifoldness of the object of their study. Thanks to Freud and his students and followers it has been recognized for some time by impartial biological spectators on the side lines that academic psychology would do well to go to school to the despised psychiatrists for awhile. Out

of all the bitter controversies which have gone on around him Freud emerges as a very great man, with many of the earmarks of genius. The publishers do well to keep this little volume in press.



LA GÉNÉRATION HUMAINE. (*Les secrets de la vie*).

By G. Mozy.

Librairie Le François

10 francs 4 $\frac{3}{4}$ x 7 $\frac{3}{8}$; 152 (paper) Paris

The first of a series designed to tell the French what they ought to know about sex. Dr. Mozy is much impressed by the terrible effects of alcohol on the offspring. "*Les expériences de Stokar et Miss Craiy*" on guinea pigs are cited; also some remarkable figures purporting to give the results of clinical observation on human subjects. "When the father alone is alcoholic, 58 per cent of sterility, 22 per cent of still-born, 20 per cent of living children, but all ill, epileptic or sickly. When it is the mother, 25 per cent of sterility, 25 per cent of still-births, 50 per cent of normal subjects." Frankly we are from Missouri about these percentages until we know something more about how they were collected than Dr. Mozy vouchsafes us.



BIOMETRY

A SOURCE BOOK IN MATHEMATICS.

By David E. Smith.

McGraw-Hill Book Co., Inc.

\$5.00 5 $\frac{3}{4}$ x 9; xvii + 701 New York

The second of a series of source books in the history of the sciences. To the biometrician the most interesting of the sources are the correspondence of Fermat and Pascal on Probability, De Moivre on the Normal Curve, Legendre on Least

Squares, Chebyshev on his inequality and Laplace on the Normal Curve.



THE PRINCIPLES OF MEASUREMENT AND OF CALCULATION IN THEIR APPLICATION TO THE DETERMINATION OF DIOPHANTINE QUANTITIES. *Bureau of Standards Research Paper No. 145.*

By Edward W. Washburn.

U. S. Government Printing Office
10 cents $5\frac{7}{8} \times 9$; 26 (paper) Washington

The ordinary treatment of the theory of errors assumes that the unknown true value sought is a member of a continuum of "possible" values. In many problems, however, the true value is known to be a member of a set of discrete values, e.g. the positive integers. This paper gives a systematic treatment of such cases.



BIOMETRICAL STUDIES OF THE GROS MICHEL BANANA. *Part I. Biometrical Technique. Bulletin No. 17. Parts II and III. The Fruit. Bulletin No. 18. Part IV. The Vegetative Growth. Bulletin No. 19.*
By A. N. Hartman. United Fruit Co.
Boston

$8\frac{1}{2} \times 11$; Bulletin 17, iii + 40 (paper)

Bulletin 18, iv + 157 (paper)

Bulletin 19, iii + 39 (paper)

A careful and detailed study of variation and correlation of bunch weight and other characters of the banana as affected by type of soil and climatic conditions. Growth curves of the banana plant under various conditions are also given.

PSYCHOLOGY AND BEHAVIOR

CONFIGURATIONAL LEARNING IN THE GOLDFISH. *Comparative Psychology Monographs Vol. 7, No. 1, Serial No. 31.*
By F. Theodore Perkins and Raymond Holder Wheeler. The Johns Hopkins Press

\$1.00 $6\frac{3}{4} \times 10$; 50 (paper) Baltimore

This study of the learning processes of goldfish was made to determine to what extent they would exhibit "insightful" activity under controlled conditions. Briefly the method of procedure was as follows. Compartments with definite light intensities were placed in aquaria in such a way that the fish were blocked off in a small area. The only way of escape was for the fish to enter one of the compartments. In the different groups of experiments the number of compartments varied and their positions shifted. Also there was a change of light intensities which varied from double bright, bright, medium, dim to dark. Food in the compartments was used as a lure. The fish were trained to choose a light of a certain intensity, being allowed to feed only in the compartment so lighted. As a means of shock a stick was stirred vigorously when the wrong compartment was entered.

Some of the conclusions which the authors draw regarding their work are as follows:

"Goldfish readily learn to discriminate between different degrees of light intensities (possibly degrees of yellow)."

"These animals seem able to detect a 'constant relationship' between the lights when the intensities are shifted upward or downward, thus indicating that their responses are configurational, or structured."

THE PSYCHOANALYSIS OF THE TOTAL PERSONALITY. *The Application of Freud's Theory of the Ego to the Neuroses. Nervous and Mental Disease Monograph Series No. 52.*

By Franz Alexander. Authorized English translation by Bernard Glueck and Bertram D. Lewin. With a prefatory note by A. A. Brill.

Nervous and Mental Disease Publishing Co.
\$3.50 New York and Washington

6 x 9; xx + 176

This book is based upon a series of nine lectures given at the Berlin Psychiatric Institute during 1924 and 1925, which have since been corrected and expanded. While primarily intended for the psychiatrist, and having for its main object the treatment of mental disease, the book will be found useful and interesting by the general biologist. The author's exposition of Freud's theory of the ego is extremely lucid and persuasive.



THE HUMAN MIND.

By Karl A. Menninger.

Alfred A. Knopf, Inc.

\$5.00 6 x 9½; xxv + 447 New York

This book is intended to explain psychiatry in simple terms to doctors, lawyers, patients and other laymen. The presentation is largely in terms of case histories. The book is attractively written and will give the reader a better understanding of his own peculiarities and a greater tolerance for those of others. There are a bibliography and an index.



THE GROWTH OF REASON. *A Study of the Role of Verbal Activity in the Growth of the Structure of the Human Mind.*

By Frank Lorimer. Harcourt, Brace and Co.

\$3.75 5½ x 8½; xii + 231 New York

To a mere biologist it appears that this

book would have been a better one if its author had not tried to do so many things all at the same time. But to drive a three-horse team *abreast*, not *tandem*, made up of psychology, philosophy, and metaphysics, needs an old and wise hand and head. The book is primarily an interesting and sound review of the psychology of infancy and childhood. Mingled with this inherently straightforward and useful job are the author's own ideas of the philosophy of society and a sort of Whiteheadian metaphysic. No objection *per se* can be made to these latter elements, at least in a free country. But it would have been easier on the reader if the author had written three books instead of one, and stuck tight to the particular subject in hand in each one. Simplicity and straightforwardness are great and rare virtues.



THE FOUNDATIONS OF EXPERIMENTAL PSYCHOLOGY.

By H. Banister, Philip Bard, W. B. Cannon, W. J. Crozier, Alexander Forbes, Shepherd I. Franz, Frank N. Freeman, Arnold Gesell, H. Hartridge, Selig Hecht, James Q. Hollopple, Walter S. Hunter, Truman L. Kelley, Carney Landis, K. S. Lasbley, Mark A. May, T. H. Morgan, John P. Nafe, George H. Parker, Rudolf Pintner, Eugene Shen, L. T. Troland, Clark Wissler. Edited by Carl Murchison.

Clark University Press

\$6.00 6 x 9; x + 907 Worcester, Mass.

This book deals with all psychological problems which, in the judgment of the editor and his collaborators, promise a reward to experimental investigation. It is their intention to revise it often enough to be always abreast of progress and to change the list of problems as emphasis in psychology changes. Among the chapters in the present edition which will be

of special interest to the biologist are the Mechanism and Laws of Heredity, by T. H. Morgan, and The Study of Living Organisms by W. J. Crozier.



LA QUESTION DES TROPISMES

By Maurice Rose.

Les Presses Universitaires de France

75 francs 6 x 9 $\frac{3}{8}$; vii + 469 Paris

This is an extremely thorough, complete, fully documented, and critical review of the literature of tropisms in plants and animals. The first and larger part of the book deals with the experimental facts; the second part with the general theories of tropistic responses, of which there are two, one associated with the name of Jennings, the other with that of Loeb. Both are thoroughly discussed, critically but fairly. Neither one is found to be entirely satisfactory. This volume will be an extremely valuable addition to any biological library.



DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 318*. Containing following articles: *Rationelle Organisation von biologischen Instituten*; and *Rationelle Technik der geistigen Arbeit des Forschers*.

By S. Tschachotin.

Urban und Schwarzenberg

6.60 marks 7 x 10; 106 (paper) Berlin

This fascicle is an example of the massive thoroughness of the great Abderhalden handbook of biological technique. The first part deals with the rational organization of a laboratory. It describes in great detail such matters as the best method of filing papers; keeping an in-

ventory; arranging the library; card cataloging everything; keeping the accounts; spurring on the *Diener* to lead a higher and better life; making the perfect card to hang on the professor's door to show how long he will be out for lunch; the making of a research program; and so on. Mr. George Biological Babbitt now has his perfect *apologia*.

The second part tells the biologist how to arrange and control his intellectual and emotional affairs. Instructions are given about how he should do his reading; take his notes; make a table of his problems; order his time; and in other ways put in order the more mechanical aspects of what is optimistically called *geistige Arbeit*. Then the higher things are discussed. The biologist is urged to organize himself and told how to do it. He should live in the suburbs; wear light and porous clothing, avoiding particularly tight and stiff collars which interfere with the free circulation of the blood to the brain; practice deep breathing; eat meats and other foods rich in phosphorus if he be engaged in original creative work, but when occupied in critical work lean rather more to a vegetable diet; do a little in the gymnastic way; sleep well; and observe moderation and regularity in the gratification of the sexual appetite. In the psychic sphere the advice is equally detailed, but we can spare no more space. The final section deals with methods of favorably influencing intuition and inspiration.



PROHIBITION AND THE BIBLE.

By George Kilpatrick.

15 cents

George Kilpatrick
Bridgeport, Pa.

3 $\frac{1}{2}$ x 6; 23 (paper)

The importance of this little pamphlet in these troubled times is indicated by the

fact that it contains "every important reference in the Bible pertaining to the drink question." The author thinks that the prohibitionists do not play fair with the Bible, because they only "partly quote" and "distort the Book to suit their own narrow views." He makes a rather strong case for this view.



THE ELEMENTS OF LOGIC.

By Robert Latta and Alexander Macbeath.

The Macmillan Co.

\$2.00 4 $\frac{3}{4}$ x 7 $\frac{1}{4}$; viii + 393 New York

A textbook of deductive and inductive logic.



THE SCEPTICAL BIOLOGIST.

By Joseph Needham.

W. W. Norton and Co., Inc.

\$3.00 4 $\frac{3}{4}$ x 7 $\frac{1}{4}$; 270 New York

A series of pleasant essays on the philosophy and history of science. The philosophical essays are largely devoted to setting forth the virtues of a dilute eyewash patented by the author and alleged to be healing, which he labels Neo-mechanism; the historical sketches treat of S. T. Coleridge as a Philosophical Biologist, Julien de la Mettrie, and William Harvey and the Witches.



THE SEA.

By H. A. Marmor. *D. Appleton and Co.*

\$3.00 5 $\frac{1}{8}$ x 8; x + 312 New York

A popular treatise on the sea in which the author, Assistant Chief in the Divi-

sion of Tides and Currents of the United States Coast and Geodetic Survey, leads the reader from a review of ancient sea lore and early maritime exploration down to the South Polar exploits of Amundsen and of the unfortunate Scott in 1911. There is summarized in an entertaining way what the science of oceanography has disclosed concerning the oceans of the earth. Some of the special topics are as follows: The depth of the sea, the bottom of the sea, the surface waters, the waters of the depths, waves of the sea, ocean currents, etc. This is a book which should prove especially useful in high school libraries. It contains 45 illustrations and figures and is well indexed.



A HISTORY OF SCIENCE and Its Relations with Philosophy and Religion.

By William C. D. Dampier-Whetham.

The Macmillan Co.

\$4.00 6 $\frac{1}{4}$ x 9; xxi + 514 New York

Like Whewell, Dampier-Whetham is interested, not in presenting a catalogue of names of scientists, as is sometimes the case with historians of science, but in tracing the development of scientific thought. His viewpoint is that "by its inherent nature and fundamental definitions it [science] is but an abstraction, and that, with all its great and ever-growing power, it can never represent the whole of existence." There are passages in the book which the reader who shies at mathematical formulae will probably skip; nevertheless even he will be well repaid by reading this interesting and intelligently written history of science.



THE COST OF BIOLOGICAL BOOKS IN 1930

By JOHN R. MINER

Department of Biology, School of Hygiene and Public Health, Johns Hopkins University

AT THE end of the first volume of THE QUARTERLY REVIEW OF BIOLOGY (Vol. 1, pp. 605-608, 1926) was inaugurated the plan of reporting annually on the cost of the books which had been received during the year. The present paper continues this plan with the report of book costs for the year 1930.

For the purpose of price comparison the books are classified by origin as follows:

I. *The United States.* Here are put all books published by strictly, or primarily, American publishers. Naturally the majority of books reviewed during the year have had this origin just as in earlier years.

II. *Germany.* In the number of books sent in by publishers for review, Germany stands next to this country.

III. *English-American.* In this group are placed the books which are manufactured in the first instance in England by publishing houses which have *branches* under their own name (not merely agents) in this country. The American branch imports the books into this country and distributes them here, priced in dollars rather than shillings.

IV. *England.* In this class are placed books published in England, priced in shillings, and available in this country only by direct importation, by the individual or through an agent.

V. *France.* This group includes all books published in France and her colonies.

VI. *Other Countries.* Here are placed all books published in any other country than those specified above.

VII. *United States Government.*

VIII. *British Government.*

Table 1 gives, for each of these eight rubrics, (a) the total number of pages in the books received for review; (b) the total cost of these books in dollars, foreign prices being converted to dollars on the basis of the exchange prevailing when the books were received; (c) the average price per page in cents.

In order to facilitate comparison in respect of book prices, Table 2 has been

TABLE 1
Prices of biological books, 1930

ORIGIN	TOTAL PAGES	TOTAL COST	PRICE PER PAGE
			<i>cents</i>
English-American.....	4,578	\$87.50	1.91
Germany.....	11,573	210.14	1.82
British Government....	1,514	17.98	1.19
England.....	5,960	67.55	1.13
United States.....	73,436	803.29	1.09
Other Countries.....	2,453	23.69	0.97
France	7,710	36.32	0.47
U. S. Government.....	4,081	12.30	0.30

prepared. In this table the following items are included: (a) the average price per page, in cents, for the years 1926-1930, (b) the absolute changes in average price per page, in cents, between 1926 and 1930, and between 1929 and 1930, a + sign denoting an *increase* in 1930 as compared with the earlier years, and a - sign denoting a *decrease*; (c) the percentage differences of the 1930 average price per page from those of 1926 and 1929, the + sign again indicating that the books were on the

average higher in price in 1930 than they were in the earlier years, and the — sign that they were lower.

The first point to be noted from Table 1 is the change from an increase to a decrease in the total amount of book material noticed in *THE QUARTERLY REVIEW OF BIOLOGY*. The total number of pages reviewed in 1930 is 111,305, a decrease of 20.6 per cent from 1929, but an increase of 34.8 per cent over 1926.

Turning to the prices given in Table 1 we find that the English-American books head the list, as in every previous year

As to the trends in prices shown in Table 2, the most noteworthy is the continued increase in the prices of German biological books. Each year, during the period for which these tabulations have been made, shows an increase over the previous year. In 1930 the German biological books of our sample were 10.3 per cent higher than in 1929, and 67.0 per cent higher than in 1926. Their present price per page is far above that of any other group except the English-American books, in which, as has been already mentioned, are included cost of transportation

TABLE 2
Comparison of the prices of biological books from 1926 to 1930

ORIGIN	AVERAGE PRICE PER PAGE					CHANGE + OR — FROM 1929 TO 1930		CHANGE + OR — FROM 1926 TO 1930	
	1926	1927	1928	1929	1930	Absolute	Relative	Absolute	Relative
	<i>cents</i>	<i>cents</i>	<i>cents</i>	<i>cents</i>	<i>cents</i>	<i>cents</i>	<i>per cent</i>	<i>cents</i>	<i>per cent</i>
English-American.....	1.55	1.39	1.46	1.90	1.91	+0.01	+0.5	+0.36	+23.2
Other Countries.....	1.51	0.78	1.13*	1.68	0.97	-0.71	-42.3	-0.80	-53.0
England.....	1.28	1.4	1.09	1.29	1.13	-0.16	-12.4	-0.15	-11.7
United States.....	1.12	1.09	1.14	1.14	1.09	-0.05	-4.4	-0.03	-2.7
Germany.....	1.09	1.20	1.48	1.65	1.82	+0.17	+10.3	+0.73	+67.0
British Government.....	—	0.96	1.26	0.39	1.19	+0.80	+205.1	+0.23†	+24.0†
France.....	0.35	0.36	0.45	0.47	0.47	0	0	+0.12	+34.3
U. S. Government.....	0.31	0.24	0.21	0.23	0.30	+0.07	+30.4	-0.01	-3.2

* With two special treatises omitted as explained in Vol. III, p. 601.

† Change from 1927 to 1930.

except 1928. It should, however, be remembered that these prices include both transportation and the United States tariff. For other groups the prices given refer to the country of publication and do not therefore include either of these charges.

As usual the biological books published by the United States Government stand at the bottom of the list. France continues to produce the cheapest commercially published scientific books, costing on the average less than half as much as those of any other country.

and tariff. French biological books, on the other hand, show no change in price from 1929. Since 1926 they have increased 34.3 per cent, but are still well below the other groups of commercially published books.

England, the United States, and the United States Government show comparatively little change over the five-year period. In 1930 prices decreased slightly from 1929 for England and the United States, but increased slightly for United States Government books. The classes British Government and Other Countries,

being comparatively small samples, have fluctuated widely from year to year, but have shown no marked trend. In general the British Government books have been on much the same price level as commercially published English books.

If all the books noticed in *THE QUARTERLY REVIEW OF BIOLOGY* in 1930, regardless of origin, are lumped together and compared with all the books noticed in earlier years it works out that the average price per page in 1926 was 1.097 cents, 1.030 cents in 1927, 1.095 cents in 1928, omitting the two very expensive books noted, 1.194 cents in 1929, and 1.131 cents in 1930. This indicates a *decrease* in average price of 5.2 per cent in 1930 as compared with 1929, but an *increase* of 3.1 per cent as compared with 1926. On the whole it is obvious that, in the period reviewed,

no violent price changes have occurred in either direction, if one envisages a generally balanced library of current biological books.

In concluding these notes for the present year, we should like again to emphasize that the statistical nature of the basic data is such as not to permit wide generalization. We are dealing here only with very small samples of books in general, and with by no means all of the strictly biological books. Indeed for some of the countries our samples are only fractions of the biological works there, published. So the reader must be cautious in the kind of conclusions he draws from these annual reviews of the experience of *THE QUARTERLY REVIEW OF BIOLOGY* regarding book prices.



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